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BREEDING ASIAN FIELD CROPS

WITH SPECIAL REFERENCE TO CROPS OF INDIA

John Milton Poehlman
University of Missouri
AND
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Line Drawings by Hannah T Croasdale

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FOREWORD – I

The present day plant breeding, with its high degree of efficiency, derives its strength from genetics, which provides the scientific basis for it The explosive growth which genetics has seen during the last 15 years has not changed in any basic way the plant breeding methods developed in earlier years, but it did have an impact In the first place, this impact has been of an indirect nature Extensive and rigorous analysis on the structure and function of genetic material, both in lower and higher organisms, has provided support for validity of the gene concept, as a unit of transcription of genetic information The resolution of hereditary elements at the gene level is obviously of great significance from the point of view of breeding studies More directly, advances in quantitative genetics have led to a clearer understanding of the components of genetic variation and of the gene actions generating them

These and other advances make it necessary that new books on plant breeding are written and new editions brought out I feel particularly happy to welcome the present edition of Professor Poehlman's well known book, for it is of special interest to us in this part of the world It is, I believe, the first comprehensive book on plant breeding, written specifically for students in Indian and other Asian universities This offers an obvious advantage. The theoretical basis for plant improvement work may be the same, but the problems which crop scientists in different parts of the world have to encounter differ considerably They differ, both as a function of the plant species to be improved, and variable requirements of the people Also, it is not possible for plant breeders everywhere to exploit always the most favourable gene interactions in the development of a strain It may often be desirable to choose an alternative, keeping in view various practical considerations

I also welcome Professor Poehlman's book for another reason The strategy for the development of scientific agriculture, which India and other countries in South-east Asia have adopted, envisages a key role for improved

varieties The present book, therefore, comes at a most opportune time, and having been privileged to see its contents, I feel sure that it will make a significant contribution to our efforts in this direction.

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Director-General
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NEW DELHI

FOREWORD – II

The power and potency of modern plant breeding research has been amply demonstrated in recent years in India The introduction of dwarfing genes in rice and wheat and the exploitation of hybrid vigour in maize, sorghum and pearl millet have all led to the opening of altogether new vistas in crop yields It has now become evident that response to fertilizer application is controlled more by morphological factors than by physiological ones Unless the variety has a morphological frame that is conducive to its cultivation in soils which are adequately fertilized and irrigated, it is not possible to get the desired response from investment in production inputs Intensive agriculture, however, brings in its wake many new problems such as the more widespread occurrence of diseases and pests and sensitivity to deficiencies of micronutrients A plant breeder has to strive ceaselessly for the improvement of the crop and for the incorporation of genes for resistance against the new physiological races of pathogens which might have arisen subsequent to the release of an earlier strain In other words, there must be a series of outstanding varieties ready in a plant breeder's assembly line, if the needs of a dynamic agricultural programme are to be met Varietal diversity and rapid varietal replacement are essential for the sustained progress of intensive agriculture

The great asset of tropical and sub tropical agriculture is the possibility of growing several crops in a year Under such conditions, the breeder should develop varieties which are most efficient when yields are measured in terms of productivity per day rather than per crop Also, it is necessary to develop varieties which would do well under conditions of drought and other adverse factors Recent genetical tools have helped us to recombine efficiently the genes present in the naturally existing populations of crop plants Where variability is restricted in the natural population, elegant techniques are available for artificially inducing mutations With the wide array of tech-

niques for the genetic manipulation of both the morphological and physiological traits of a crop plant now available, scope exists for tailoring a crop plant to the needs of a specific purpose

In India, as well as in several of the developing nations, there is much protein malnutrition in addition to insufficiency of calories The recent discovery by Purdue scientists that the Opaque 2 and Floury 2 genotypes in maize are associated with a high lysine content represents a major breakthrough in the development of cereal varieties with a desirable protein quality In many regions of the world, enhancement of the quality of food through a shift to the plant-animal man food chain would not be easy in view of the already existing scarcity of grains and the rapidity of growth of the population The animal food chain is too expensive in terms of energy conversion and it is here that there is urgent need for varieties of cereals and grain legumes high in the content of amino acids in short supply, such as methionine and tryptophan There are distinct possibilities that this can be done, provided a country is endowed with knowledgeable and dedicated plant breeders

To be a successful plant breeder, it is necessary to have intimate contact with the plants one is working with The eminent plant breeder Dr Norman E Borlaug of Mexico once mentioned "plants speak to men but only in whisper, their voice can be heard only by those who remain close to them" To develop this type of affinity with the plant, it is necessary to train one's eye as well as mind A thorough knowledge of the principles, methods, purposes and philosophy of plant breeding is essential to become a skilled plant engineer A good plant breeder can exert a catalytic effect on the whole cycle ol agricultural development, as is evident from the recent trends in agrarian advance in India Dr Poehlman hence deserves the gratitude of all those who stand to benefit from progress in plant breeding research, for the excellent book he has written on the breeding methods useful in the improvement of field crops Dr Poehlman s book carries the authority of many years of experience of an exceedingly successful plant breeder, noted both for his theoretical soundness and practical achievements It therefore fulfils an important felt need of our educational institutions in agriculture and plant sciences

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PREFACE

This book is a revision and adaptation of the text "Breeding Field Crops" and is written specifically for use by B Sc degree students in agricultural botany and plant breeding in the countries of south and southeast Asia The need for such a text is very great The first edition of "Breeding Field Crops" was written for the undergraduate course in plant breeding as taught in the agricultural colleges and universities of the U S A and Canada Although widely used around the world, many of the examples in it do not really apply in the tropical climates where crops and crop varieties are vastly different and where agriculture is less developed and less mechanized The present text has been developed to adapt it to the students in this environment While designed for the introductory level of teaching in plant breeding, it may also be used to supplement the advanced or post-graduate courses and as a reference book for plant breeders working in the field The revision is being made and the text will be reprinted under the auspices of the Joint Indian American Standard Works Programme The stimulus for initiating the revision was provided by an Agricultural University Workshop held at Ludhiana, Punjab in February, 1965 At this workshop the need for developing agricultural texts to meet local Indian conditions, including the revision of standard foreign texts in collaboration with an Indian author, was discussed The authors are pleased that they were requested to develop a revised edition of "Breeding Field Crops" to meet this need in the subject of Plant Breeding

This text concentrates on the principles, procedures, and problems in the breeding of field crops in south and southeast Asia Since there are excellent Indian textbooks in Botany and many excellent textbooks in the field of Genetics, the botany of crop plants and genetic principles have been held to the minimum required for understanding the breeding procedures and the emphasis has been placed on the principles and the utilization of this fundamental knowledge in the practical breeding of crop plants It is easy to

teach the beginning student elegant genetical theory and leave him totally unfamiliar with what constitutes a good variety or how to develop one This pitfall we have tried to avoid

The selection and testing of experimental strains and varieties at high fertility levels and with optimum moisture has been stressed throughout While a large portion of the total crop acreage of India, Pakistan and neighbouring countries is now and in the immediate future will continue to be grown on soils of marginal fertility, or with inadequate soil moisture, yet the mounting pressure for food production is so great in this area of the world, that greatly increased use of fertilizers and irrigation water is inevitable It is on the tracts where improved cultural practices are used that the major benefits from improved varieties will be obtained It is therefore a folly and a waste of economic resources to breed varieties for response to poor cultural practices

In the development of the text practical examples have been chosen from local agriculture wherever possible Most of these will come from Indian agriculture for two obvious reasons India has more research stations which have been functioning for a longer period of time than adjacent countries of Asia Also, the experience of the authors has been more intimately associated with India than the other countries In the citation of references we have tried to reflect the world wide contributions to the literature of plant breeding as well as the contributions from the Asian countries concerned Since this text is primarily to teach plant breeding to the beginning student, no attempt has been made to supply a comprehensive list of references on any subject, but rather to select those that would contribute most to the intellectual development of the student

Much of the information presented here has been obtained by personal interview and it is impossible to identify all of the individuals from whom it was obtained We are particularly grateful to the respective staffs of the Botany Division of the Indian Agricultural Research Institute and the Rockefeller Foundation, New Delhi, Punjab Agricultural University, Ludhiana, Central Potato Research Institute, Simla and Jullundur, Jute Agricultural Research Institute, Barrackpore, Sugarcane Breeding Institute, Coimbatore, Madras Agricultural College and Research Institute, Coimbatore, Indian Council of Agricultural Research, Regional Research Centre (PIRRCOM), Coimbatore, Central Tobacco Research Institute, Rajahmundry, Central Rice Research Institute, Cuttack, International Rice Research Institute, Los Baños, Philippines, and the Hawaiian Sugar Planters' Association Experiment Station, Honolulu

The authors wish to thank the U S Administration for International Development (AID) for making this publication possible, the United States Information Service and the Ministry of Education, Government of India for including it in the Joint Indian American Standard Works Programme, the University of Missouri and the Department of Agriculture, Assam, for provid-

ing leaves to the authors from regular duties to complete this assignment, to Orissa University of Agriculture and Technology, Bhubaneswar for provid ing a base from which to work, and to each Dr B P Pal and Dr M S Swaminathan for writing a foreword

J M POEHLMAN
COLUMBIA, MISSOURI, U S A

15 January, 1968

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JORHAT, ASSAM, INDIA

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1

The Plant Breeder and His Work

The production of food is the problem of major concern throughout all of south and southeast Asia With the rapidly expanding populations in this area of the world the food supply, already grossly inadequate, needs to be expanded greatly in the years ahead It is not sufficient, however, only that more food be produced Along with the total caloric intake the nutritional level of the diet of the people also needs to be improved This will require the production of a greater variety of crops, particularly those that store large quantities of protein and oil, and eventually the production of more forages so that animal products may assume a larger portion of the people's diet

In addition to growing field crops for food to be consumed as grain or oil, or as forage by animals, crops are grown for fibre and other commercial products Cotton jute and tobacco crops are grown on large acreages in south and southeast Asia and are important factors in the economy of this area

To increase crop production four important inputs must be given major attention water, fertilizer, pest control and crop variety The first three, water, fertilizer and pest control, relate to providing a better environment in which to grow the crop The fourth, the crop variety, relates to the inherent ability of the plant to produce within the environment provided In other words, better plants and larger food production may result both by providing a better environment for the crop or from improvements in the heredity of the crop Most simply, the latter is accomplished by breeding better varieties

Maximum crop production cannot be reached either by use of superior production practices or by breeding better varieties, without some consideration of both (Fig 1 1, 1 2, 1 3) Rice yields in most of south and southeast Asia have been among the lowest in the world Attempts to increase the hectare yield of rice by addition of fertilizers have been only moderately successful since the widely grown indica types of this area lodge easily and do not respond favourably to the higher rates of fertilization As more nitrogen is added the lodging is increased and yields may even be further depressed To correct this situation a concerted effort is now being made to develop short, stiff early maturing, nitrogen responsive varieties of rice for tropical Asia that will stand without lodging and give progressively higher yields with increased rates of nitrogen fertilizer These practices, use of superior varieties, and increased fertilization, combined with other good cultural practices, have been responsible for the high yields of rice in Japan, Taiwan, and the U S A Use of superior varieties or hybrids, high fertilization, and pest control have been responsible also for the high yields of wheat, corn, soybeans and other grains in the U S A which have been shared in recent years with countries of south and southeast Asia short in food grains

The use of double-cropping systems in which two or more crops are grown the same year is another means for increasing crop production The successful manipulation of these rotations often hinges upon the availability of early maturing varieties to facilitate the change in the next crop, to make maximum utilization of available soil moisture or to use more economically available irrigation water

As progress in mechanization is made, new developments in harvesting machinery necessitate the development of varieties adapted for their use The combine could not be used to harvest grain sorghum in the U S A until dwarf, erect varieties were developed Soybeans that shattered their seed

upon ripening were unsuited to combine harvesting and American breeders found it necessary to develop new varieties that would hold their seed until harvest New cotton varieties had to be developed which could be more efficiently harvested by mechanical means before the cotton picker was fully successful

Disease epidemics are not static The spread of new diseases or of new forms of old diseases necessitates persistent efforts toward breeding of varieties with greater resistance The spread of the sereh disease of sugarcane threatened to wipe out the sugarcane industry of Java until a resistant variety was found Frequent shifts in the forms of the cereal rusts have necessitated persistent efforts in order to maintain resistant varieties

Hereditary improvements in crop varieties may be made in several respects The improved variety may be more vigorous in its growth thus producing a higher yield through the more efficient use of the plant nutrients available to it It may stand until harvest with less loss from lodging or shattering Plant characteristics may be altered so that a satisfactory yield may be harvested when environmental conditions over which the cultivator has no control are unfavourable Thus the breeder strives for early maturity increased resistance to heat drought disease and insect damage The new variety may produce grain oil or proteins with improved nutritional value Such hereditary improvements are more or less permanent by planting improved varieties the benefits may be reaped over and over All of these present a challenging future to the plant breeder

WHAT IS PLANT BREEDING?

Plant breeding is the art and the science of changing and improving the heredity of plants

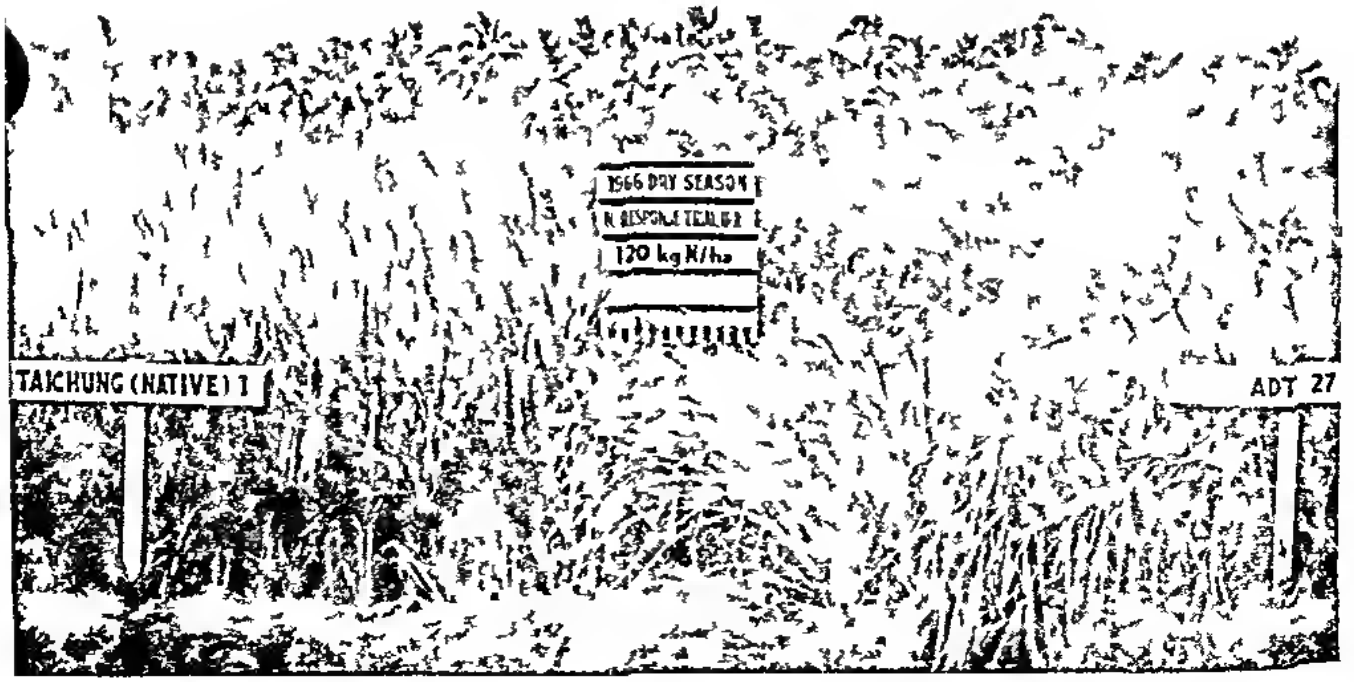


Fig 1 1 Varietal response to fertilization of rice at the International Rice Research Institute the Philippines At left the short nitrogen responsive variety Taichung Native 1 remains erect after application of 120 kg N/hectare while the native indica variety at right is heavily lodged

Fig 1 2 Water management to provide irrigation during the dry season and to provide drainage during the monsoon season is important to good crop yield Here Dr S P Kohli wheat breeder Indian Agricultural Research Institute adjusts the flow of irrigation water to his experimental wheat plots

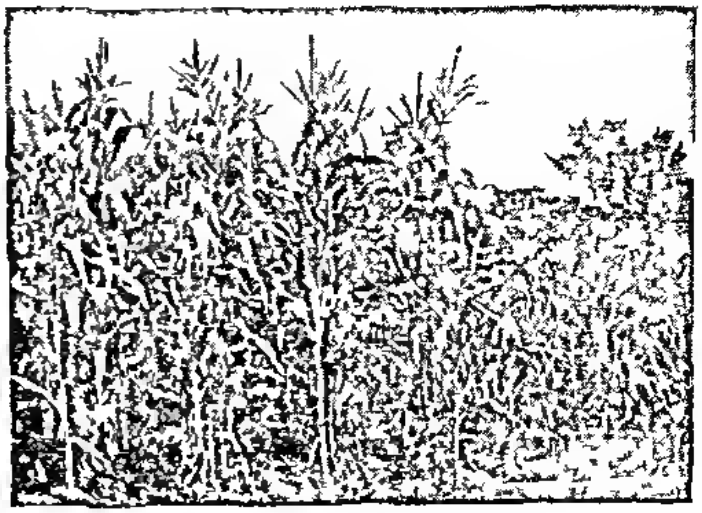


Fig 1 3 Good breeding in maize is shown by the vigorous growth of this experimental plot being grown as part of the India Coordinated Maize Breeding Scheme

In earlier days the extent of plant breeding as an art and as a science was much disputed Plant breeding was first practiced when man learned to select the better plants, thus selection became the earliest method of plant breeding The results of man's early efforts in plant selection no doubt contributed much to the course of development of many of the cultivated crops, however little he may have been conscious of his efforts in the beginning As man's knowledge about plants increased, he was able to select more intelligently With the discovery of sex in plants, hybridization was added to his breeding techniques Although hybridization was practiced before the time of Mendel, its significance in inheritance was not clearly understood until Mendel's experiments came to light and laid the basis for an understanding of the mechanism of heredity

The art of plant breeding lies in the ability of the breeder to observe in plants differences which may have economic value Before breeders possessed the scientific knowledge that is available today, they relied largely on their skill and judgment in selecting the superior types Many breeders were good observers, quick to recognize between plants of the same species variations which could be used as the basis for establishing new varieties For them plant breeding was largely an art Many of the early breeders were amateurs, a cultivator who found an off type plant in his field or a gardener who found a sport in his beds Some, like Luther Burbank, were professionals who searched far and wide for unusual plant types which could be developed and exploited commercially

As the breeders' knowledge of genetics and related plant sciences progressed, plant breeding became less of an art and more of a science No longer was it necessary for the breeder to rely so completely on his skill in finding chance variations with which to establish new varieties It now became possible to plan and create new types more or less at will His scientific knowledge gave him the background to manipulate and direct the inheritance of plants Although skill in the art of selection is important to the modern plant breeder, just as it was to the breeder in the past, now skill alone is not enough Modern plant breeding is based on a thorough understanding and use of genetic principles It requires a knowledge of plant diseases and their epidemiology and of physiological factors affecting the adaptation of plants Without this precise knowledge and background, the modern breeder could neither explore nor comprehend the vast range of the problems involved He could, as did the early breeders, resort only to hit or miss methods in breeding, which are costly and time-consuming He would be like a village blacksmith trying to build a modern automobile with only the crude tools of the blacksmith trade

TRAINING FOR THE MODERN PLANT BREEDER

The student may ask What do I need to study to become a plant breeder? The simplest answer that can be given is that *You need to study plants*" (Fig 1 4) But the study of plants is divided into many branches, and numerous fields of plant science as well as other closely related disciplines, are embraced in the training of the modern plant breeder Important areas of knowledge, in which it is essential that the modern breeder have training, and their relations to plant breeding are

1 *Botany* The plant breeder should be an accomplished botanist so that he will understand the taxonomy, morphology, and reproduction of the plants with which he works

2 *Genetics and cytogenetics* The plant breeder needs a thorough understanding of the mechanism of heredity in plants since modern plant breeding methods are based on a knowledge of genetic principles and chromosome behaviour

3 *Plant physiology* Variety adaptation is determined by the response of plants to their environment This includes the effects of heat, cold, drought and soil nutrient response

4 *Plant pathology* Varietal resistance is an important means of combating many plant diseases

5 *Entomology* Breeding for insect resistance is receiving increasing attention by plant breeders

6 *Plant biochemistry* Suitability for industrial utilization often determines the market demand for a particular variety of a crop Examples are the milling and baking qualities of a wheat variety, the cooking qualities of a rice variety, or the fibre qualities of a cotton variety Many chemical and physical tests are required to test varieties for these qualities Knowledge of biochemistry is also contributing toward a better understanding of mutation and gene action

7 *Statistics* The plant breeder measures the comparative performance of many strains Sound field plot techniques and methods for statistical analyses of data are necessary to obtain reliable results and to interpret the results correctly The understanding of quantitative inheritance is also based on a knowledge of statistical procedures

8 *Agronomy* Above all, the breeder of field crops should be a good agronomist *He should know crops and their production* He should understand what the cultivator wants and needs in the way of new varieties, so that he may be able to evaluate the breeding materials available to him and plan a breeding programme in the light of these needs

Fig 1 4 Distinguished plant breeders examine a field of rice at the Central Rice Research Institute Cuttack India They are (from left) Dr R H Richharia former Director Central Rice Research Institute, Dr N Parthasarathy FAO Regional Rice Improvement Specialist Dr B P Pal Director General Indian Council of Agricultural Research and Dr K Ramiah Vice Chancellor Orissa University of Agriculture and Technology Dr Parthasarathy and Dr Ramiah are also former Directors of the Central Rice Research Institute

These sciences are the tools with which the plant breeder works The plant germ plasms available to the breeder are his raw materials The breeder uses his knowledge of the sciences to create from the raw materials new and improved varieties of crops, just as the engineer uses his knowledge of mathematics, physics, or chemistry in the construction of a new bridge or a modern skyscraper

It is apparent that the plant breeder cannot be a specialist in all these fields of plant science In the practice of plant breeding he is not working exclusively in any of them The work of the plant breeder is to apply the whole of his knowledge and experience toward the development of superior varieties If he should need additional information about the inheritance of a plant character with which he is working or about a technique for measuring the resistance of plants to some environmental condition, he may conduct experiments to study those specific problems so that he may more intelligently conduct his breeding work Such specialized research is not necessarily plant breeding, but the information gained may help him

in the guidance and direction of his breeding research Oftentimes a breeder may combine theoretical experimentation in one or more of these fields with his breeding studies This broadens his understanding of these areas of knowledge and their relation to his particular breeding problems, and so may be a desirable conjunction with a breeding progamme Since the improvement of an important field crop like maize, or wheat, or cotton usually involves several of these fields of plant science, specialists in genetics, plant pathology, and entomology work cooperatively with the plant breeder Most of the spectacular accomplishments in plant breeding are now the result of such teamwork, with each specialist contributing to the work in his field and the plant breeder coordinating the whole to the end that a superior agronomic variety may be developed

SOME EARLY PLANT BREEDERS

Just when man consciously began to breed plants is difficult to establish It is known that the date palm was artificially pollinated by the Assyrians and Babylonians as early as 700 B C The red Indian did a remarkable job of plant breeding with the maize plant, long before the white man reached the American shores However, the fact of sex in plants was not established with certainty until the work of Camerarius, whose studies were reported in 1694 As the function of the pollen in the fertilization of plants became known, interest increased in the crossing of varieties and species of plants

The first artificial plant hybrid was made by Thomas Fairchild, who crossed the sweet william with the carnation about 1717 The hybrid plant obtained from this cross is commonly known as Fairchild's mule An American, Cotton Mather, observed in 1716 that ears from yellow maize planted next to red and blue maize would have red and blue kernels scattered among them This appears to be the first recorded observation of natural hybridization Systematic studies of artificial plant hybridization were carried out by a German, Joseph Koelreuter, between 1760 and 1766 He made many crosses with tobacco and kept an accurate account of his work An Englishman, Thomas Andrew Knight (1759 1835), was one of the first men to use hybridization for practical plant improvement A horticulturist, Knight produced many new kinds of fruit and garden crops by cross pollination

The methods which plant breeders use in breeding new varieties today have slowly evolved from the contributions of a large number of men beginning with the first demonstration of sex in plants by Camerarius The work of only a few of them can be reported here

According to DeVries (1907), John Le Couteur, an English breeder, and Patrick Shirreff, a Scottish agriculturist, were the first to use the progeny test During the middle of the nineteenth century both worked with cereals and used the progenies of single plants to establish new varieties The principle of using the progeny to establish the breeding value of a plant was the subject of intensive study by a Frenchman, Louis Leveque de Vilmorin, who published the results of his work in 1856 Studies on the sugar beet were continued by his son, Henry de Vilmorin

The principle of individual plant selection to establish varieties of self pollinated crops was developed at the plant breeding station of the Swedish Seed Association, Svalof, shortly before 1900 Dr Hjalmar Nilsson, who became director of the station in 1890, by careful observation and painstaking record keeping, soon established the fact that only the progenies of single plants would be uniform and that the entire plant was the correct basis for selection, not a single spike or a single grain The latter view had been advocated by Frederic F Hallett, an Englishman, who practiced selection of the best spike from a plant of wheat and selection of the best seed from that spike The theory of the single plant or pure line selection method received confirmation by the Danish botanist Johannsen, whose work with garden beans was published in 1903 Willet M Hays, a breeder of this period who worked in the U S A, also established independently the value of using progenies of single plants to establish uniform varieties Hays developed the "centgener" method of testing progenies in which a hundred seeds were spaceplanted in an area of one square meter About the same time the 'rod row" method of testing small cereals was developed In the rod row method of testing, varieties are grown in rows one rod (or more generally 16 feet) in length It is now common in the U S A and many other countries to use shorter plots, usually 8 to 10 feet in length, for

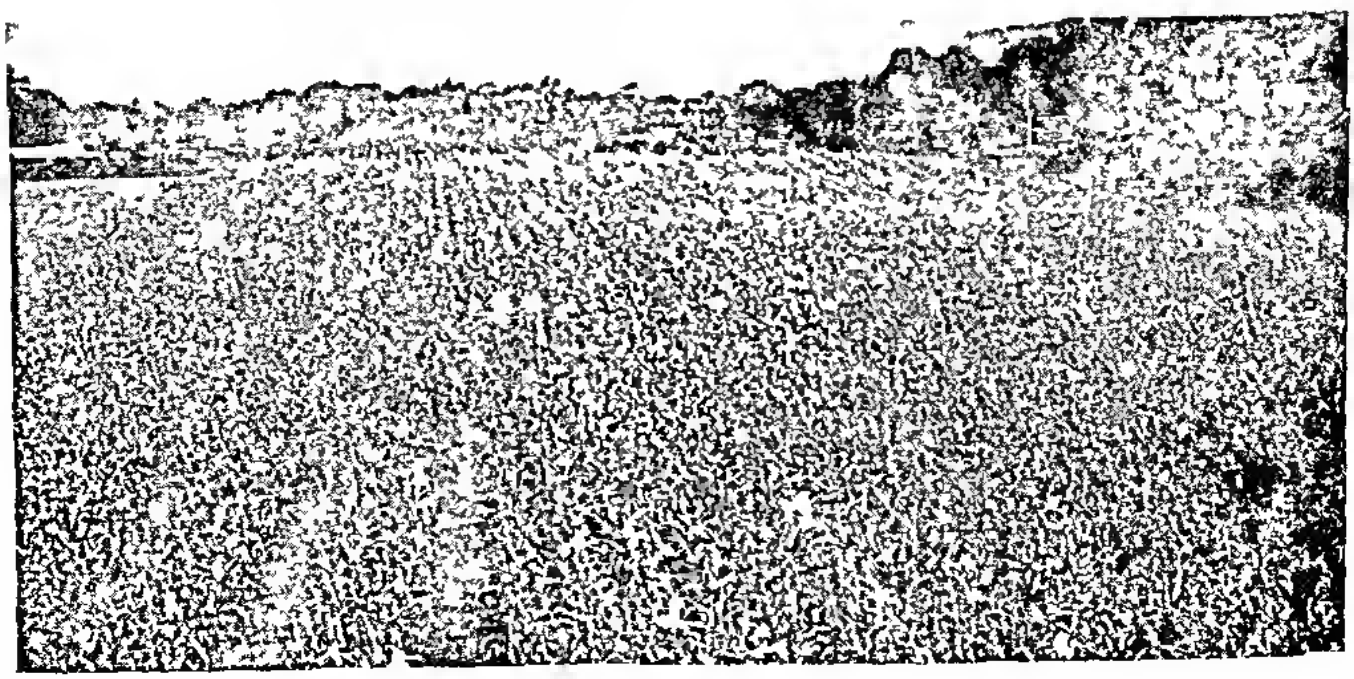
preliminary testing of varieties and strains of small cereals like wheat or barley

While a great number of early hybridizers were active during this early period and later, none made as important a contribution as the Augustine monk, Gregor Mendel, who studied the inheritance of the common garden pea His was the first authoritative interpretation of the simple facts of inheritance Through keen observation and clear reasoning he established a few simple principles of inheritance Although published in 1866, the work of Gregor Mendel was unnoticed for over thirty years The report of his experiments was redis covered in 1900, and since then the principles he established have been enlarged and supplemented by a wealth of additional knowledge Collectively, these facts related to the phenomena of inheritance comprise the large and growing branch of science known as *genetics*, upon which plant breeding leans so heavily

The discovery of the record of Mendel's experi ments in 1900 opened up a new vista to plant breeders For the first time there were scientific principles upon which to base breeding experiments The work of Mendel stimulated much re search into the methods of inheritance in plants A direct result of one of these studies was the formulation of the present method of breeding hybrid maize Dr G H Shull started experimenting in 1904 by inbreeding strains of maize He continued to self pollinate and develop those inbred lines of maize even though their vigour at first declined with each succeeding generation But when these weak inbred lines of maize were crossed, they produced "single cross" hybrid maize more vigorous and productive than the open pollinated varieties from which they had originated Similar results were obtained by his contemporary, Dr Edward East The "double cross" (a cross between two single crosses) was suggested by Dr Donald F Jones in 1918 and was the step that made possible the production in America of hybrid seed in quantity at a price the American farmer could afford (Fig 1 5) The high potential for food production of hybrid maize is now being brought to south and southeast Asia through a cooperative Inter-Asian Maize Improvement Programme and the utilization of hybrid vigour has been extended to the breeding of sorghum, bajra, wheat, and other crops

Important advancements in forage crop breed ing were made by the contributions of Dr T J Jenkin From his work at the Welsh Plant Breeding Station, which began in 1919, the concept of strain building was developed Strain building is a

Fig 1 5 First commercial field of double cross hybrid maize This field of Burr Learning double cross hybrid maize was grown on the farm of George Carter at Carter Hill, Clinton Connecticut U S A in 1921



system of breeding in which individual plants are chosen and combined into synthetic varieties on the basis of their breeding behaviour

SOME ACCOMPLISHMENTS IN CROP BREEDING

The improvements made in field crops by plant breeding are numerous Examples of them will be cited throughout this text to illustrate for you ways in which the important crop plants have been made more productive and safer to grow A few of these improvements merit special consideration

The yield and sugar content of Indian sugarcane varieties has been built up by the hybridization of "noble" canes with native types Local strains of *Saccharum barberi* origin, largely grown in northern India, could survive the rigours of the north India environment but they were generally unproductive and their sugar content was low The tropical "noble" canes of *Saccharum officinarum* origin were larger and more productive, thicker stemmed and higher in sugar content, but would not grow well in the soil and winter climate of north India In 1912 a sugarcane breeding station was established at Coimbatore Dr C A Barber and his successors, Dr T S Venkatraman and others, at Coimbatore, by intercrossing of these two types and the wild species, *Saccharum spontaneum*, have developed canes of high yield and sugar content adapted to the climate of north India Co (Coimbatore) canes are now grown in all of the major sugarcane areas of India and in other areas of the world

An improvement in wheat production in the southern Great Plains of the U S A came about by the chance introduction of Turkey Red wheat Taken to the U S A by a small group of Mennonites who emigrated from Russia and settled in central Kansas in 1873, this "hard' wheat was found to be well adapted to the Great Plains It was hardy and produced good yields in spite of cold and drought From this small introduction and later introductions of Turkey type wheats by the United States Department of Agriculture, there was established the hard red winter wheat industry that has made the central and southern Great Plains of the U S A the bread basket of the world

In India, pioneer work on the improvement in yield and quality of wheats by breeding was begun by the Howards in the early 1900's Strains of Pusa and NP (New Pusa) wheats they selected from indigenous stocks became famous for their yielding ability and quality The studies of Dr K C Mehta in the early twenties on the epidemiology of the black stem rust revealed the role of the hill wheats of north India in the spread of this ravaging disease to the plains below Although the spores of the rust were killed by the high summer temperatures in the plains, they could survive on the stubble or on wheat or other hosts at the higher altitudes Thus rust infection started in the hills would spread to the foothills and later to the plains as the season advanced This led to an intensive programme for breeding rust resistant hill wheats by Dr B P Pal and his associates which still continues

The production of combine sorghum has been built from two short plants of milo The first was a mutant dwarf plant found in a field of Standard Yellow milo From this plant a new Dwarf Yellow milo variety was born which soon replaced much of the taller parent variety A few years later a second and even shorter dwarfed plant appeared as a mutation in the dwarf variety Soon a Double Dwarf Yellow milo variety was being grown Similar dwarfed plants were later found in other varieties These dwarf sorghums have entered into the parentage of all the short combine varieties, which are now grown so extensively throughout the southern and central Great Plains Now they are providing basic germ plasm for a hybrid sorghum improvement programme in India

Many improvements in varieties have been made by breeding for disease resistance Two notable early accomplishments are the work of Orton in breeding for wilt resistance in cotton and that of Bolley in the breeding of wilt resistance in linseed Both workers subjected plants to a natural epidemic of the disease by growing them in wilt-infected soils and selected surviving plants (Fig 1 6) This principle of survival is basic in disease resistance breeding today Orton reported his work in 1899 The work of Bolley followed in 1901

Substantial progress in breeding for stem rust resistance in wheat was made by McFadden, who in 1916 made an interspecific cross between an emmer and a common wheat One of the resulting spring wheat varieties was called Hope, even though it was undesirable in yield and quality But the name was prophetic From Hope and its sister selection, H-44, came the genes that for more

than a decade protected a major portion of the spring wheat area in the U S A from the ravages of that dreaded disease, "black stem rust"

No report on the spectacular breeding improvements in crops would be complete without mention of hybrid maize Its origin as a genetic study has already been reported From its inception, with the reports by Dr G H Shull in 1908 and 1909, until actual commercial production of maize hybrids was attained on a large scale throughout the American Corn Belt about thirty years later, contributions were made by many plant breeders, geneticists, and seedsmen Thousands of inbreds were produced and fitted together in various combinations in order to find the ones that would be most productive A hybrid seed production industry was developed which could increase the superior hybrids in quantity and make them available to the American farmer The development of hybrid maize ranks foremost among the many breeding accomplishments of the present century, and it has led the way for the utilization of 'hybrid vigour' in many other crop plants

The benefits from hybrid maize and sorghum are now being realized in India and other countries of south and southeast Asia where coordinated hybrid maize and hybrid sorghum breeding projects have been organized Through the cooperative efforts of many governmental organizations and the Rockefeller Foundation in India, hybrids adapted to many areas in south and southeast Asia are being developed

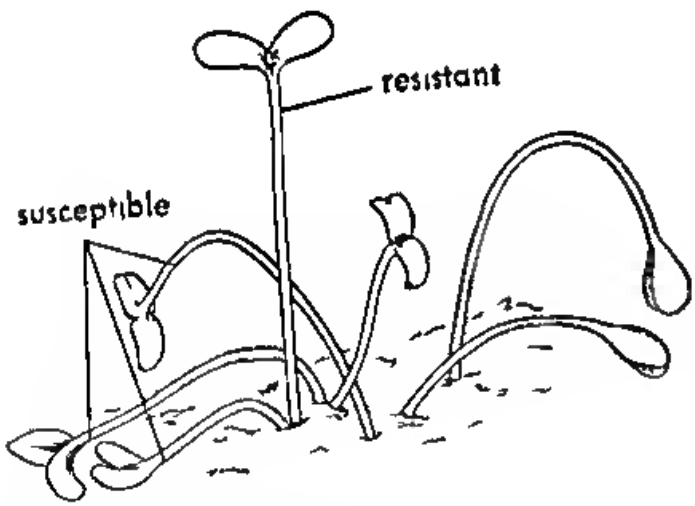


Fig 1 6 Young flax plants that have wilted because of early attacks of the w lt fungus from flax sick soil In 1901 Dr H L Bolley North Dakota Agr cultural Experiment Station reported that the wilt fungus was the cause of this d sease By select ng surviving plants growing in infected so l Dr Bolley developed wilt resistant varieties of flax The principle of survival is basic in disease resistance breed ing today

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2

Reproduction in Crop Plants

The breeding procedures that may be used with a particular crop species are determined by its mode of reproduction This relationship will become clearer as the breeding methods used with the various crop species are studied in more detail However, it may be illustrated here quite simply by comparing the seed production practices of two common crop plants, rice and maize, which differ in their pollination method In rice, a self pollinating crop, the seed of an improved variety may be harvested and planted over and over again if, *during its production, reasonable care is exercised* in the maintenance of varietal purity Since rice pollen fertilizes the flower in which it is borne, no new genetic factors are introduced which may disturb the purity of a variety Contrast this with hybrid maize, a cross pollinated crop In the seed production of hybrid maize, pollination is controlled by detasseling or by other means which permit natural cross-pollination between carefully selected lines Hybrid vigour is expressed to the greatest extent in the first generation of these controlled crosses So the cultivator must buy new seed each year if he is to obtain maximum yields The system of breeding hybrid maize was readily adapted to the maize plant on which the pollen-bearing organ is borne in the tassel and the egg-bearing organ is borne on a lateral shoot By the use of male sterility, similar systems of breeding have been adapted to other cross pollinated crops Without a clear understanding of the details of pollination, fertilization, and seed development for a crop plant it would not be possible to develop orderly and efficient breeding procedures It is necessary, therefore, that the breeder thoroughly acquaint himself with the details of the mode of reproduction in the particular crops with which he is working Knowledge of the details of reproduction is important also because it provides a basis for understanding the mechanism of heredity in plants Basically, it is from the knowledge of genetic behaviour that the breeding system for a particular crop species is devised

TYPES OF REPRODUCTION

Reproduction in crop plants may be by seeds, *sexual,* or by vegetative parts, *asexual* With sexual reproduction specialized reproductive cells, called gametes, are formed This process is known as *gametogenesis* Fusion of the male and female gametes leads to the development of an embryo and eventually the seed In asexual reproduction new plants arise from specialized vegetative organs such as tubers, rhizomes, runners, bulbs, corms, or by various means of propagation such as rooting of plant cuttings, grafting, or layering Most field crops reproduce by sexual means (seeds) although asexual reproduction is common with some crops

SEXUAL REPRODUCTION IN CROP PLANTS

A wide degree of genetic variability cannot be created or maintained in plants, except through their sexual reproduction The importance of the process to the breeder is so great that it is reviewed here in detail

Parts of the Flower. The flower contains the sexual reproductive structures of the plant It commonly consists of four floral organs, *sepals*, *petals*, *stamens*, and *pistil* (Fig 2 1) Typically, the petals are large and brightly coloured, the sepals are small and inconspicuous Petals and sepals are not necessary for reproduction Only the stamens and the pistil function in the production of seeds The stamen usually consists of a slender stalk or *filament* which supports an *anther* Within the anther

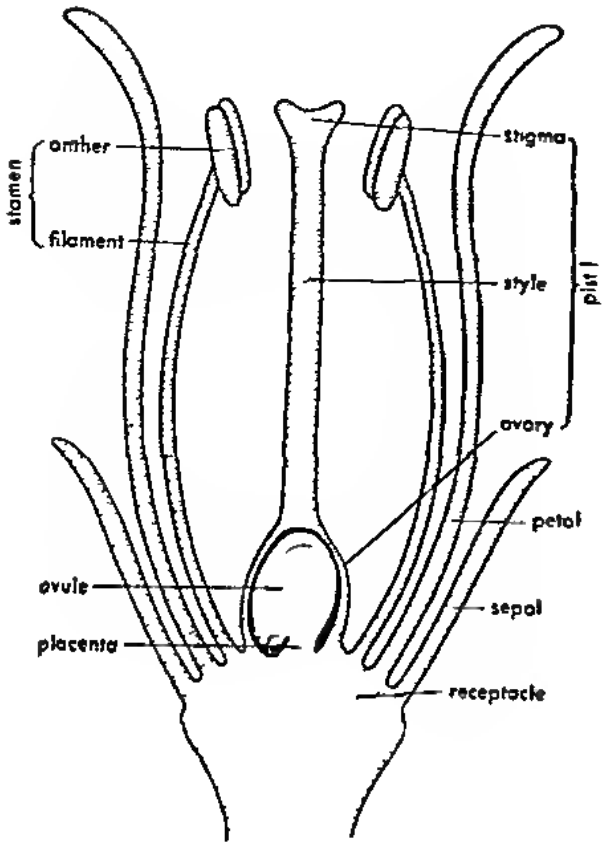


Fig 2 1 Parts of the flower

the pollen grains develop The pistil commonly consists of an enlarged base or *ovary* in which the seeds are formed, an elongated stalk or *style*, and a *stigma* on which pollen may be deposited Within the ovary are found the ovules or immature seeds which after fertilization develop into the mature seeds The number of ovules within an ovary may vary from one, as in wheat or rice, to several hundred, as in tobacco

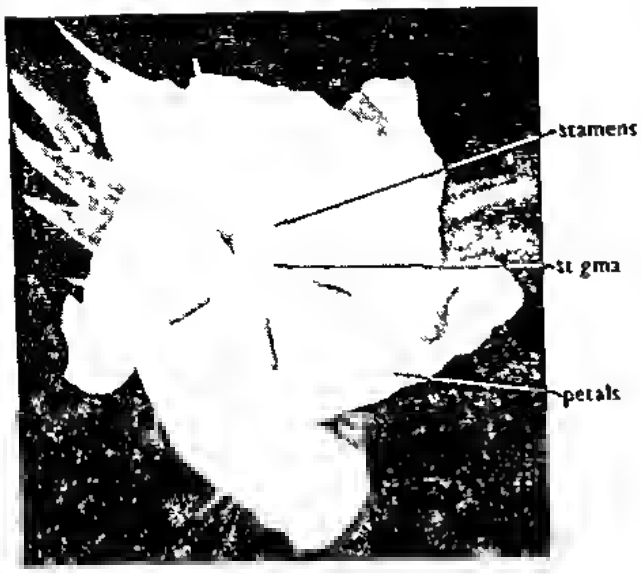
Kinds of Flowers. *Complete* flowers contain all four floral organs (sepals, petals, stamens, pistil) *Incomplete* flowers lack one or more of these floral organs Complete flowers are borne on cotton, linseed, tobacco, rape, potatoes, soybeans, red clover, lucerne, sesame, betel, and many other crop plants (Fig 2 2) Crops belonging to the grass family, including maize, sorghum, wheat, barley, oats, rice, and the common hay and pasture grasses, have incomplete flowers in which the petals and the sepals are lacking (Fig 2 3) In groundnut *cleistogamous* flowers, inconspicuous flowers which do not open, are frequently produced below the ground level[3*] Cleistogamy also may occur in some of the grams

Perfect flowers bear stamens and a pistil in the same flower structure, but one of these essential organs is absent in *imperfect* flowers Most crop plants have perfect flowers Examples are rice, wheat, oats, barley, rye, sorghum, cotton, linseed, tobacco, sugarcane, soybeans, and most common forage grasses and legumes Imperfect flowers may be *staminate*, bearing stamens but no pistil, or *pistillate*, bearing a pistil but without stamens The maize plant has staminate flowers in the tassel and pistillate flowers on the shoot. Crop plants in which staminate and pistillate flowers are borne on the same plant, as in maize, colocasia, ramie or castor, are *monoecious* (Fig 2 4), crop plants in which the staminate and pistillate flowers are borne on different plants are *dioecious* (Fig 2 5) Hemp, hops, and papaya are species with dioecious flowers Hemp also produces some monoecious flowers Imperfect flowers are always incomplete Some incomplete flowers, such as occur in rice, wheat and many other grasses, are perfect since both the stamens and a pistil are present in the same flower although petals and sepals will be missing

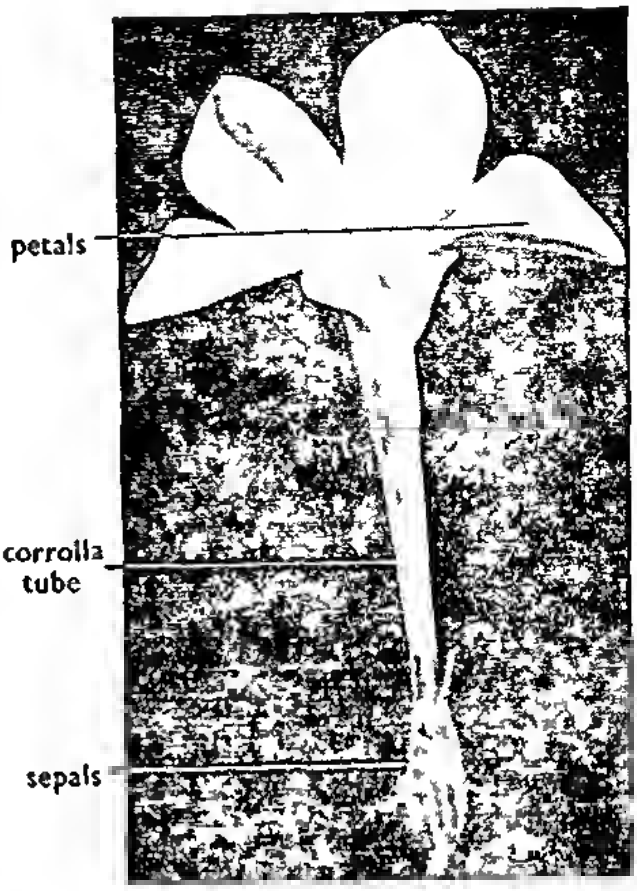
Pollination and Fertilization. Seeds are formed within a plant by a succession of processes in which the stamens and the pistil play important roles The steps in the reproductive cycle leading to the formation of a seed are reviewed here briefly (Fig 2 6) Within the immature anther are four cavities containing many *microspore* or *pollen mother cells* Each mother cell undergoes two successive nuclear divisions and forms a tetrad of four *microspores* Each microspore may develop into a *pollen grain* The microspore is transformed into a pollen grain by a thickening of the spore wall and a division of the microspore nucleus to form a tube cell nucleus and a generative nucleus As the anther matures the pollen sacs open and the pollen grains are dispersed The pollen grains are produced in great numbers, from twenty to fifty million may be produced on the tassel of a single maize plant.

Pollination is the transfer of the pollen grains from the anther to the stigma The means of transfer varies with different crops Pollen from the anther of the maize plant is carried by the wind Some of it may fall on the stigma of the same plant, although

* Superior numbers refer to references cited at the close of chapters.



2 2A



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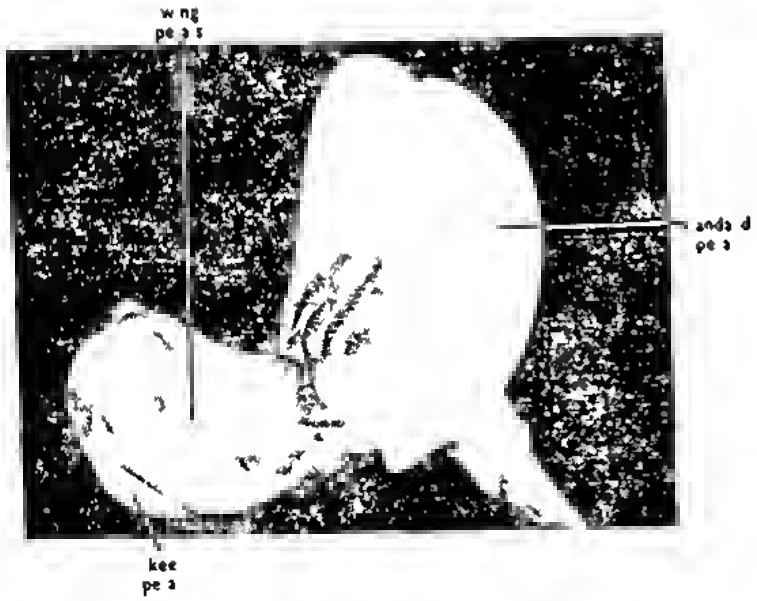

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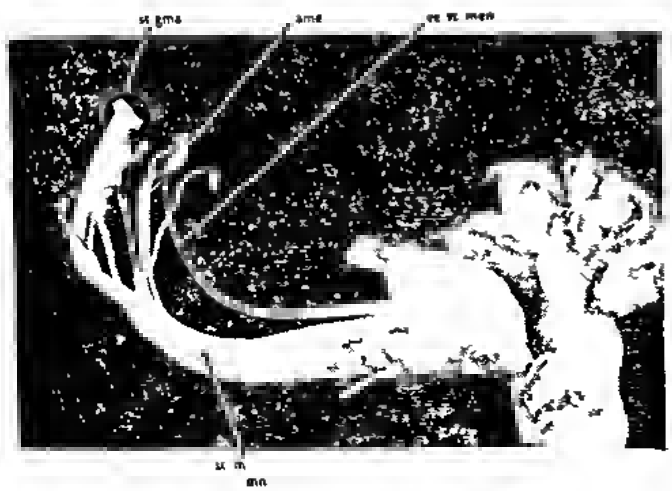
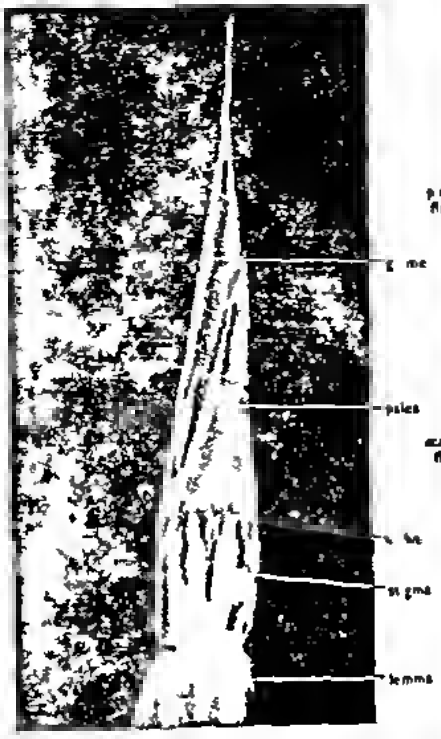


2 2D

Fig 2 2 Complete flowers A Flower of cotton showing whorl of five petals stamens and stigma The sepals are hidden by the petals B Flower of tobacco showing sepals and five petals The petals are fused and form a corolla tube surrounding the stamens and the pistil C Flower of the cowpea typical of the flowers in the legume family The corolla is composed of one standard two wing petals and two keel petals D Flower of the cowpea with all petals removed In the typical legume flower nine stamens form a staminal column which surrounds the stigma The tenth stamen remains free

2 3A



2 3B

Fig 2 3 Perfect and incomplete flowers A Flowers of buckwheat *Fagopyrum esculentum* lacking petals The sepals are white to greenish white B The flower of grasses lacks petals and sepals In the oat flower shown here the lemma is pulled down to expose the stigma and the anthers The lemma and palea form the hull which covers the kernel in oats

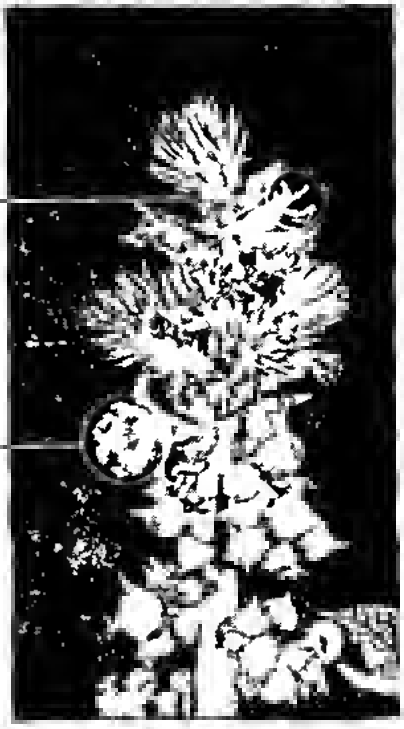


Fig 2 4 Monoecious flowers of the castor plant

Fig 2 5 Dioecious flowers of papaya A Staminate inflorescence B Pistillate inflorescence

2 5A

2 5B

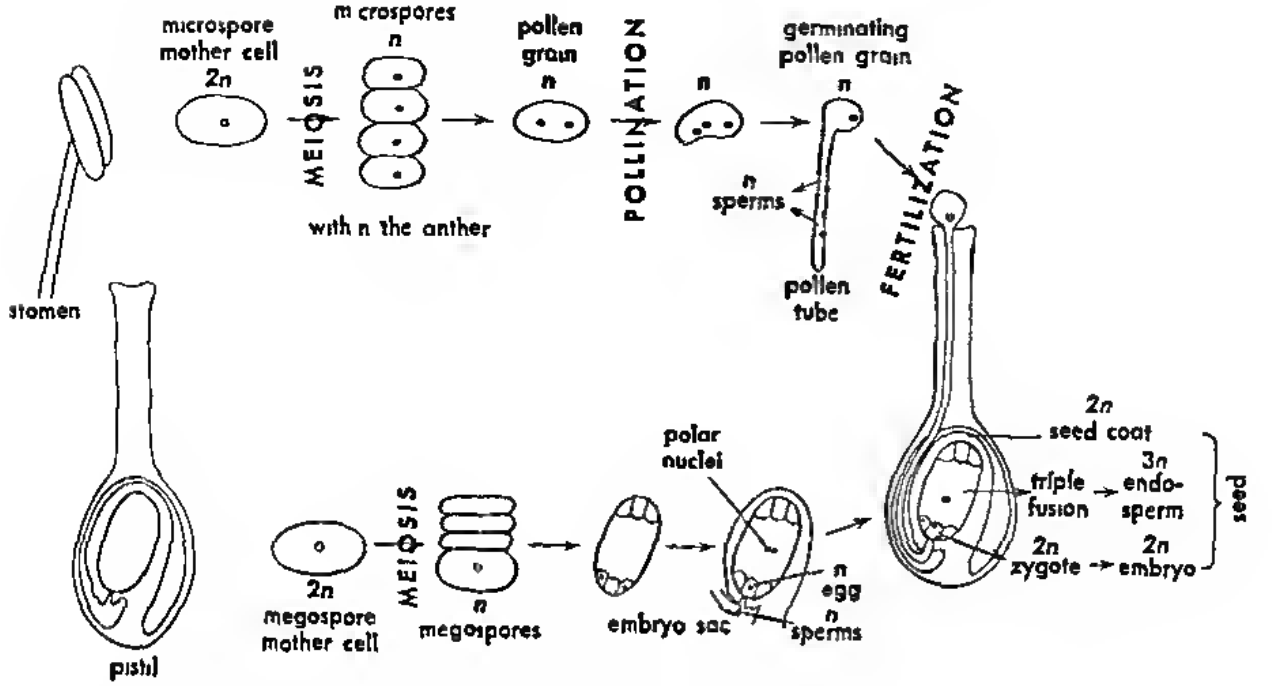


Fig 2 6 Steps in the reproduction of a seed plant Starting with the spore mother cells in the anthers and in the ovules a succession of events takes place which leads to fertilization and eventual formation of a seed

it is more likely that the stigmas will be pollinated with pollen from surrounding plants The forage grasses, rye, and sugarcane are also pollinated to a large extent by wind borne pollen In many legumes, such as berseem and lucerne, the pollen is carried from one flower to another by insects In the pulses, wheat, and many other crops some of the pollen usually is shed directly upon the stigma within the same flower as the anthers open In wheat, oats barley, and rice the stamens and the pistil are enclosed by floral bracts which tend to prevent pollination from other flowers The stigma is the portion of the pistil that is receptive to the pollen It may be branched or feathery, so that it catches the pollen grains in its branches, or it may secrete a sticky stigmatic fluid to which the pollen grains adhere The pollen germinates on the stigma and a slender *pollen tube* grows through the style and enters the tip of the ovule through an opening known as the *micropyle* Two male germ cells, called *sperms*, are formed by division of the generative nucleus of the pollen grain The sperms move through the pollen tube and are emptied into the embryo sac (Fig 2 6)

The female germ cell, or gamete, is produced within the ovule by a succession of steps similar to those which led to the production of the sperm (Fig 2 6) Within each ovule is a single *megaspore mother cell* which, like each of the microspore mother cells, undergoes two successive nuclear divisions and produces a tetrad of four megaspores Three of the megaspores disintegrate One of the megaspores, usually the megaspore farthest from the micropyle, continues to undergo nuclear divisions and forms an ovoid, eight nucleate *embryo sac* The female gamete or *egg* and two additional nuclei (synergids) lie near the micropyle, three nuclei (antipodals) lie in the opposite end of the embryo sac, the two remaining nuclei, termed *polar nuclei,* lie in the central area After the two sperms are emptied from the pollen tube into the embryo sac, one sperm fuses with the egg to form a *zygote*, a process known as *fertilization* The second sperm unites with a nucleus which was formed by the earlier fusion of the two polar nuclei or all three of these nuclei may fuse simultaneously The nucleus resulting from this *triple fusion* is called the *primary endosperm nucleus* These processes, in which both sperm nuclei function, is referred to as *double fertilization*

The *seed* has its beginning with the fertilized egg (zygote) and the endosperm nucleus The fertilized egg develops into the *embryo* which, on germination of the seed, grows into the new plant The primary endosperm nucleus divides many times to form numerous nuclei nuclei become enclosed by cell walls to [illegible] *perm*, a

tissue in which starch, oil, or protein is stored This stored food supplies the germinating embryo and the early stages of seedling growth In the cereals the larger part of the seed is endosperm In seeds of gram, groundnut, and other legumes the endosperm is absorbed by the developing embryo and the food materials are stored in *cotyledons* The *seed coat* develops from integuments surrounding the ovule

Nuclear Division and Chromosomes. A plant is composed of small structural units called *cells* A typical cell is composed of a viscous material known as *cytoplasm* surrounded by a wall A *nucleus* is embedded within the cytoplasm along with various other inclusions With the aid of a microscope and with proper staining techniques, shortened rod-like *chromosomes* may be observed within the cell nucleus during nuclear division Two types of nuclear division occur (Fig 2 7) One form of division, *mitosis* (equational division), is normally characterized by

1 The lengthwise duplication of each chromosome to form two chromatids

2 The disappearance of the nuclear membrane and the formation of a spindle of fibres

3 The movement of the chromosomes to the quator of the spindle

4 The migration of the chromatids to the opposite poles of the spindle

5 The formation of two daughter nuclei, each with a complement of chromosomes similar to those present in the parent nuclei

6 The formation of partitioning cell walls between these daughter nuclei

Cytologists recognize several phases of the mitosis division process but *of significance here is the fact that the daughter nuclei normally receive duplicates of each chromosome originally present in the nucleus of the parent cell* Mitosis is the method of division by which new cells are formed in the normal growth and development of the plant It is the only form of cell division associated with asexual reproduction

The second form of nuclear division, *meiosis*, is associated with sexual reproduction in the plant Meiosis occurs when the spore mother cells divide to form the spores and consists of two successive divisions, the first reductional and the second equational Meiosis is characterized by

1 Duplication of each chromosome lengthwise to form two chromatids

2 Pairing of *homologous chromosomes*, i e , those which have genes that control similar hereditary characteristics, and formation of chiasmata or the interchange of corresponding segments between homologous chromosomes

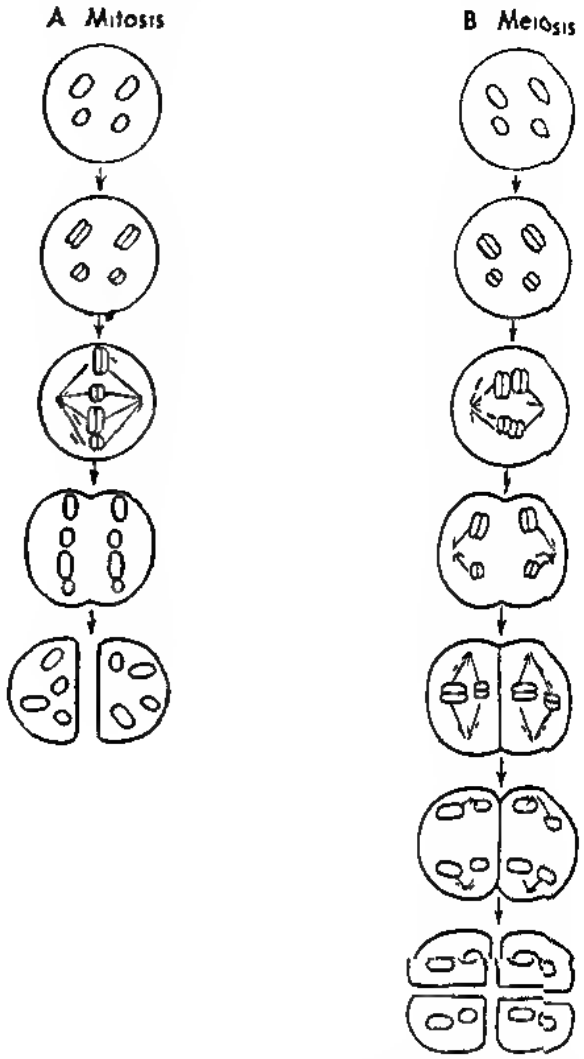


Fig 2 7 Comparison of mitosis (A) and meiosis (B) A In mitosis two daughter cells are formed with chromosomes identical with those in the parent cell B In meiosis four daughter cells are formed each with the haploid chromosome number

3 Movement to the equator of the spindle of the homologous chromosomes with their chromatids still joined together at regions known as *centromeres*

4 Separation of the homologous chromosomes with a member of each pair moving to opposite poles with their chromatids still joined (reductional division)

5 The formation of new spindles in each end of the cell with the joined chromatids becoming arranged at the equator of each of the spindles

6 The division of the centromeres and the migration of the chromatids to the poles of their respective spindles (equational division)

7 The formation of cell walls to form four spores, each with half as many chromosomes as the parent spore mother cell

As with mitosis cytologists recognize a number of phases in the process of meiosis *An essential feature of meiosis is the reduction of the chromosome number from the diploid* (2*n*) *number in the mother cells to the haploid* (*n*) *number in the spores* Since gametes are formed from the spores by successive mitotic divisions, they will contain the haploid chromosome number also The sperm and the egg fuse at fertilization, and the diploid chromosome number is restored in the zygote The endosperm nucleus is formed by the triple fusion of a sperm with the polar nuclei and has a triploid (3*n*) chromosome number Meiosis is important in maintaining a stable chromosome number in a species otherwise the chromosome number would be doubled with each generation when the two gametes fuse The chromosome number in the individual cells starting with the spore mother cells and ending with the formation of the seed, is illustrated in Figure 2 8

Other events of significance to the plant breeder that occur at meiosis are, (*a*) the segregation of contrasting genes or alleles and subsequent re combination of characters in individuals in the succeeding generation, and (*b*) crossing over as the result of chiasmata formation which leads to a recombination of linked genes These phenomena will be discussed in more detail in the next chapter

Chromosome Numbers in Crop Plants. The diploid chromosome numbers of some crop species commonly cultivated in south and southeast Asia are listed in Table 2 1 The haploid diploid chromosome number is essentially constant for any plant species It may be noted that two of the cultivated species of wheat, *Triticum durum* and *T aestivum*, have chromosome numbers of $2n=28$ and $2n=42$, respectively Certain wild species of *Triticum*, *T boeoticum* for example, have chromosome numbers of $2n=14$ Thus the haploid chromosome numbers of the three species, *T boeoticum*, *T durum*, and *T aestivum*, are 7, 14, and 21, respectively A group of closely related species like these in which the chromosome number is increased in an arithmetic ratio constitutes what is known as a *polyploid* series Polyploidy and its significance in plant breeding will be discussed more fully in the next chapter and in the chapters on specific crops that have a polyploid origin In a naturally occurring polyploid series, the species with the higher chromosome number is generally the more vigorous and productive It is sometimes possible to form polyploids by adding together the chromosome complements of two species or by doubling the chromosome number in plants This is accomplished by application of an organic chemical, *colchicine*, to the actively dividing cells in the growing tip, and by other means These techniques are being used to produce new strains of forage crops and new giant varieties of common flowers, and also to breed

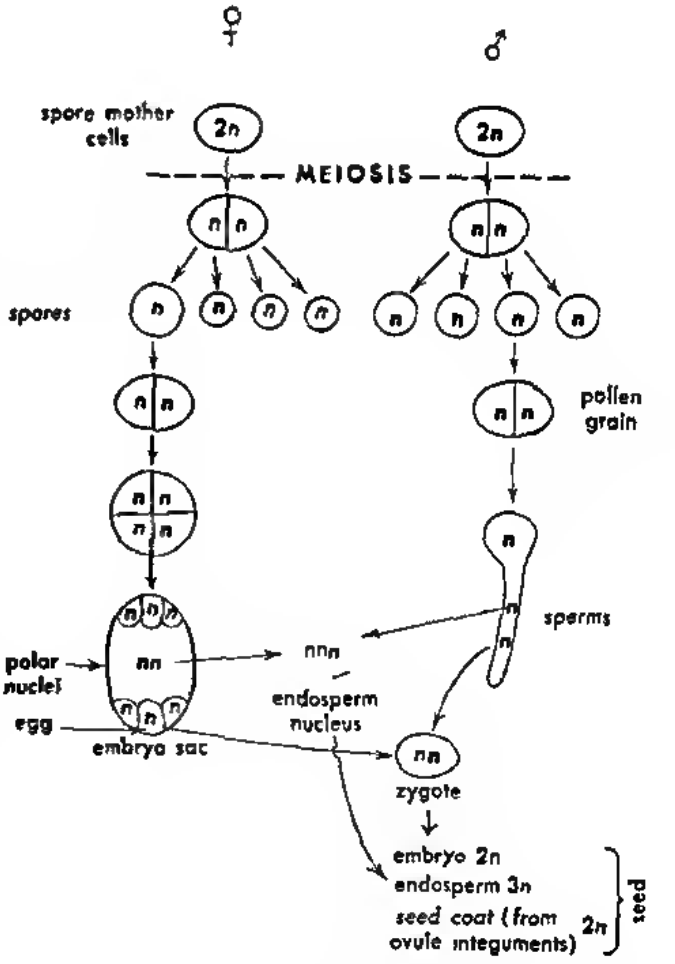


Fig 2 8 Diagram showing haploid diploid and triploid chromosome numbers in cells of the reproductive organs of a seed plant

other plant species as will be discussed in chapters which follow

Self- and Cross-Pollination in Crop Plants. *Self-pollination* is the transfer of pollen from an anther to a stigma within the same flower or to a stigma of another flower on the same plant Cereal crops, such as wheat or rice in which the flower is enclosed by floral bracts, are seldom pollinated except from pollen originating in an anther within the same flower This is in contrast to the pollination in the maize plant, in which pollen is carried by the wind to silks of other plants, or to the pollination of berseem flowers by insects which carry pollen from one plant to the stigmas in flowers on other plants *Cross pollination* is the transfer of pollen to the stigma in a flower on a different plant Fertilization resulting from the union of a sperm and an egg (gametes) produced on the same plant is *self fertilization* The union of a sperm and an egg (gametes) from different plants is *cross fertilization*

From the breeding standpoint, field crop plants which reproduce by sexual means may be grouped according to their usual method of pollination as *normally self pollinated, normally cross pollinated,* or *both self and cross pollinated* These groups are not distinct since slight cross-pollination often occurs in the crops normally classified as self-pollinated, and some self pollination usually occurs within the normally cross pollinated crops The amount of natural crossing or natural selfing within these crops will vary with (*a*) the variety or strain of the crop, (*b*) the seasonal conditions, (*c*) the velocity and direction of the wind, and (*d*) the insect population

Crops Normally Self-pollinated. Some common crop plants that are normally self pollinated are

barley	linseed
barnyard millet	oats
bengalgram (chickpea)	pigeon pea
blackgram	potato
cowpea	ragi
foxtail millet	rice
greengram	sesame
groundnut	soybean
jute	tobacco
lentil	wheat

The amount of natural cross pollination that may occur within crops of this group may vary from

Table 2.1. Diploid Chromosome Numbers of Some Crop Species Commonly Cultivated in South and Southeast Asia

Crop	*Species*	*Diploid (2n) Chromosome Number*
	Cereal Crops	
barley	*Hordeum vulgare*	14 ✓
maize (corn)	*Zea mays*	20 –
millet, barnyard	*Echinochloa frumentacea*	36
millet, finger (ragi)	*Eleusine coracana*	36
millet, foxtail	*Setaria italica*	18
millet, pearl (bajra)	*Pennisetum typhoides*	14 ✓
oats	*Avena sativa*	42
rice	*Oryza sativa*	24
rye	*Secale cereale*	14
sorghum (jowar)	*Sorghum vulgare*	20 –
wheat, durum	*Triticum durum*	28 –
wheat, common	*Triticum aestivum*	42 –
	Fibre Crops	
cotton	*Gossypium hirsutum*	52
hemp	*Cannabis sativa*	20
jute	*Corchorus capsularis*	14
jute	*Corchorus olitorius*	14
ramie	*Boehmeria nivea*	28
	Forage Crops	
bermudagrass (dhub)	*Cynodon dactylon*	36,40
berseem (Egyptian clover)	*Trifolium alexandrinum*	16
clover, red	*Trifolium pratense*	14
guineagrass	*Panicum maximum*	18,36
lucerne (alfalfa)	*Medicago sativa*	32
ryegrass, Italian	*Lolium multiflorum*	14
sudangrass	*Sorghum sudanense*	20

Table 2 1 (*continued*)

Crop	*Species*	*Diploid (2n) Chromosome Number*
	Oilseed Crops	
castor	*Ricinus communis*	20
linseed (flax)	*Linum usitatissimum*	30
mustard	*Brassica juncea*	36
niger	*Guizotia abyssinica*	30
rape	*Brassica campestris*	20
safflower	*Carthamus tinctorius*	24
sesame (til)	*Sesamum indicum*	26
sunflower	*Helianthus annuus*	34
	Pulses and Legumes	
cowpea	*Vigna unguiculata*	22,24
gram, bengal (chickpea)	*Cicer arietinum*	16
gram, black	*Phaseolus mungo*	22 ✓
gram, green (mung)	*Phaseolus aureus*	22 ✓
groundnut (peanut)	*Arachis hypogaea*	40
pigeonpea	*Cajanus cajan*	22,44,66
soybean	*Glycine max*	40
	Starch Storage Crops	
cassava	*Manihot esculenta*	72
colocasia (dasheens, tara)	*Colocasia antiquorum*	28,36,48
potato	*Solanum tuberosum*	48
sweet potato	*Ipomoea batatas*	90
	Stimulant Crops	
betel	*Piper betle*	32
tobacco	*Nicotiana tabacum*	48
	Sugar Crops	
sugarcane	*Saccharum officinarum*	80
sugarcane	*Saccharum barberi*	82,90,92, 116,124

none up to 4 or 5 per cent The plant breeder working with self-pollinated crops will need to determine the extent of the natural crossing under his particular conditions The percentage of natural crossing in a crop may be estimated by a simple procedure Two varieties are selected that are pure for different forms of a character which is easily recognized and simply inherited The varieties are planted in such a manner that individual plants recessive for the character are completely surrounded by plants dominant for the character Then the progenies of the recessive plants are grown to determine the percentage of plants which exhibits the dominant character

There are a number of floral mechanisms in plants which may exclude cross pollination and thereby result in a particular species being normally self pollinated Examples of these mechanisms are [2]

1 The flowers may not open

2 The pollen grains may be shed before the flowers open

3 The stigma and stamens may be hidden by floral organs after the flowers open

4 The stigma may elongate through the staminal column shortly after the anthers open

The flowering process is called *anthesis* This process in the rice plant, a typical self-pollinating cereal crop, is briefly described [1] Each rice flower is enclosed by an outer glume or *lemma*, and an inner glume or *palea* The sexual organs of the rice flower consist of six stamens and a pistil, the latter having two styles and many stigmatic branches which give a feathery appearance (Fig 2 9) At the time the stigma matures and is receptive to the pollen, two small sacklike organs at the base of the ovary, known as the *lodicules*, swell and cause the flower to open At anthesis the stamen filaments elongate, and as the flower opens, the anthers generally push out of the glumes The anthers rupture and are emptied of their pollen, part of the pollen falling inside, and the remainder outside the flower The pollen grains usually germinate within a few minutes after falling on the stigma hair, and the pollen tube starts growing in the style immediately (Fig 2 10) The time required for the pollen tube to reach the embryo sac may vary from 20 minutes to 2 hours, depending upon the temperature If the anthers do not produce viable pollen, or if the flower opens [illegible] extruded before they [illegible]

pollen to reach the stigma and bring about cross-pollination In barley and soybeans cross pollination seldom exceeds one half per cent although in rice, wheat, and tobacco cross pollination may sometimes reach as much as 2 or 3 per cent Any condition, environmental or otherwise, which disrupts the normal process of anthesis may result in a higher proportion of natural cross pollination in a normally self pollinated species

Fig 2 9 Sexual organs of rice flower consisting of six stamens and two-branched feathery stigma

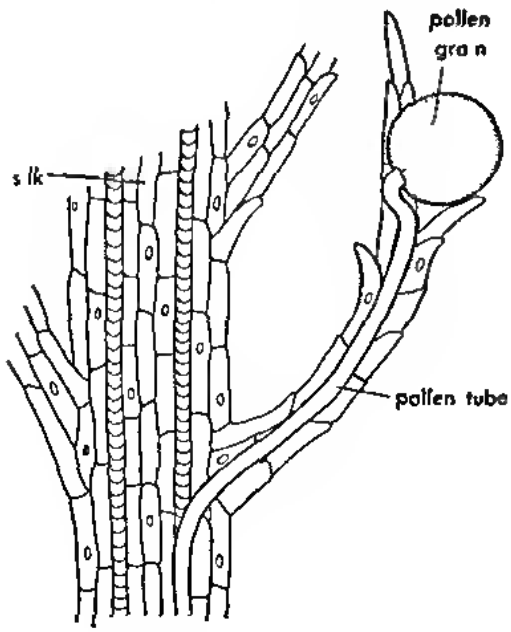


Fig 2 10 Germinating pollen grain on silk of corn

Crops Normally Cross-Pollinated Some crops that are normally cross pollinated are

berseem	niger
betel	pearl millet
bermudagrass	ramie
castor	rape
colocasia	red clover
guineagrass	rye
lucerne	safflower
maize	sunflower
mustard	sugarcane

Characteristics in flowers that may exclude self pollination thereby resulting in normal cross pollination include (*a*) mechanical obstruction to self pollination, (*b*) different periods of maturity in the pollen and the stigma, (*c*) self sterility or incompatibility, (*d*) presence of monoecious or dioecious flowers [2]

Maize is a typical monoecious plant bearing staminate flowers in the tassel and pistillate flowers in the shoot The pollen is wind borne Cross-pollination is the rule, although self pollination may reach 5 per cent or more Castor also bears monoecious flowers (Fig 2 4) with pollen both wind and insect borne Bajra has both perfect and staminate flowers The stigmas emerge several days before the anthers and are normally pollinated before the anthers dehisce Sugarcane is largely cross-pollinated from wind borne pollen Rape and mustard are mostly cross pollinated as a result of insects carrying the pollen and self incompatibility within the species although some forms may be largely self pollinated Considerable sterility or incompatibility is found after self-pollination in species of *Trifolium* (red clover and white clover), lucerne and perhaps other legumes and some grasses In these crops the pollen tubes often grow down the styles of self pollinated flowers so slowly that the ovules may disintegrate before fertilization is completed It has also been observed in lucerne and other legumes that the embryos abort after self fertilization more frequently than after cross fertilization

Dioecious crops, such as hemp, hops papaya, or buffalograss, are necessarily cross pollinated since

the staminate and pistillate flowers are borne on separate plants Dioecious crops are sometimes considered as a distinct group from a plant breeding standpoint

Crops Both Self- and Cross-Pollinated. Cotton and sorghum are the principal crops in this group, although pigeonpea might be included also Cotton and sorghum are largely self pollinated, but varying amounts of cross pollination occur The stigma in the flower of the cotton plant is exposed, and cross pollination may occur as a result of insects carrying the pollen Pollen of the cotton plant is heavy and sticky and is seldom wind borne Cross pollination in cotton normally ranges from 5 to 25 per cent although amounts up to 50 per cent have been reported in some areas where insects are abundant The sorghum crop is normally about 5 per cent cross pollinated Cross pollination in sorghum usually results from flowers opening and exposing the stigma before the pollen is shed

ASEXUAL REPRODUCTION IN CROP PLANTS

The normal method of propagating crop plants is by seeds But some crops produce seeds so poorly that vegetative propagation is resorted to as a means for their increase The potato is propagated vegetatively by tubers Stem sections or setts are used as a means of propagating sugarcane (Fig 2 11) Sugarcane produces seed abundantly only in favourable climatic locations Bermudagrass sets seed so poorly that it is often propagated entirely by vegetative sprigs Many forage species with succulent stems, such as lucerne or berseem may be vegetatively propagated by rooting stem cuttings This is practical only on a small scale as in a breeding programme Likewise rice may be vegetatively propagated on a small scale by separation and rooting of individual tillers A group of plants which is propagated vegetatively from a single plant is called a *clone* All of the plants within a

2 11A

2 11B

Fig 2 11 Asexual reproduction in sugarcane A Bud or eye at node on stem of sugarcane B Section from stem of sugarcane with shoots and roots developing from nodal buds Stem sections like these are used to propagate sugarcane in the field

clone are identical in heredity and bear the characteristics of the original parent plant Plant breeders may use clonal propagation to establish lines when the parent stocks will not breed true from seeds, or cannot be established easily from seeds

Apomixis. Apomixis is a type of reproduction in which the sexual organs or related structure take part, but in which seeds are formed without union of the gametes Seeds formed in this manner are vegetative in origin Various forms of apomixis may occur In one form, termed *parthenogenesis*, the embryo develops directly from an unfertilized egg If the chromosome number of the gamete has been reduced in the normal manner at meiosis and chromosome doubling of the unfertilized gamete does not occur, the apomictically produced embryo and the plant developing from it will be haploid If the chromosome number of the gamete is unreduced as a result of some abnormal occurrence during meiosis, the apomictically produced embryo and plant will be diploid *Apogamy* is another form of apomixis in which the embryo develops from haploid nuclei other than the eggs Commonly, apogamy results from the fusion of two cells of the embryo sac In *apospory*, the embryo sac is formed directly from a somatic cell, without reduction and formation of spores The embryo then develops directly from the diploid egg without fertilization Although sexual union does not occur in the development of apomictically produced seeds, pollination may be necessary to initiate the development of the endosperm

In some species of grasses, particularly bluegrass, *Poa pratensis*, and dallisgrass, *Paspalum dilatatum*, seed is produced largely by apomictic means It is important that a plant breeder be informed of the tendency of a species to produce seed by apomixis to avoid confusion and error in breeding experiments Crosses attempted in apomictic species would generally produce progenies like the mother plant This phenomenon may also have advantages for the breeder A superior plant type which produces seed by apomictic means will usually breed true for the characteristics of the mother plant.

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3

Genetics in Relation to Plant Breeding

Plant breeding is the application of genetic principles to the improvement of plants In this chapter we are concerned with the basic genetic principles employed by the plant breeder An understanding of these genetic principles is basic to understanding how the plant breeder can improve the heredity of the plant

VARIATION, THE BASIS OF PLANT BREEDING

Plants differ in many ways It may be safely generalized that no two plants are exactly alike, even though we may limit our observations to a single species For an example let us look at a field of maize Upon casual examination we may be impressed with the similarity of the plants within the field There is a certain constancy of features among the maize plants the development of the stalks, the size, shape, and arrangement of the leaves on the stalk, the termination of the stalk in a tassel, the formation of ear shoots at nodes midway of the stalk, and many other developmental features By these and other characteristics we recognize the maize plant and distinguish it from a plant of wheat, or tobacco, or cotton But if we should compare two plants of maize in minute detail and make careful observations and quantitative measurements of the separate plant parts, we would find that individual plants differ in many respects This would be the case even though the field were planted to a single cross hybrid, which would be as nearly uniform in heredity as we could obtain within a commercial field of maize If we were to examine plants from a wide range of varieties of maize, we would expect to find even greater variations There would be differences in maturity, height, seedcoat colour, endosperm colour, sugar content of the kernel, presence of plant pigments, disease resistance, and many more features both qualitative and quantitative in nature A correspondingly wide range of variability may be found within other species of cultivated crops

Environmental Versus Heritable Variations. Variations within a crop species are of two kinds (*a*) variations due to environment and (*b*) variations due to heredity

Environmental variations may be discerned by growing plants with similar heredity in different environments A rice plant growing in infertile soil will not grow as large and vigorous as would one of similar heredity in fertile soil A variety of maize adapted and productive in a northern latitude will respond unfavourably to the shorter days in a southern latitude and will make an unsatisfactory growth in the latter region Two seeds of oats, one large and one small, will produce seedling plants differing in size because the small kernel has less stored food material to start the seedling plant, even though the genetic composition of the two seeds may be identical Two plants of wheat from the same pure strain will differ in development and yield if one is severely infected with black stem rust while the other is protected from this disease These variations in growth and development result from the effects of the particular environment in which the plants are grown Corresponding variations are not necessarily observed in their progenies

Hereditary variations are the result of plants possessing different genetic characters Generally, they may be observed if different varieties or species are grown under similar conditions Hereditary variations may be simple and easily observed seed or plant characters, such as differences in colour of the plant or seed, amount of pubescence on the leaf or stem, presence or absence of awns, or type of endosperm The variations may be more com-

plex characteristics, such as vigour of growth, tillering capacity, disease resistance, height of plant, or date of maturity Since these variations are inherited, they are expressed again in the progeny, although the intensity with which they are expressed may vary with the environment A yellow-seeded variety of mustard differs from a brown-seeded variety If pure it will produce only yellow-seeded progeny Dwarf sorghum plants are shorter than standard sorghum plants when both varieties are grown in a similar environment favourable for sorghum production If a mixed lot of wheat is grown in an environment suited to the development of stem rust and all plants become infected with the disease except one, we may assume that the healthy plant differs from the diseased one by being inherently resistant or immune and that the diseased plants are susceptible This assumption may be verified by growing the progeny of the healthy plant in an environment favourable for the development of rust and observing whether or not the progeny becomes diseased If non rusted plants are observed in the progeny of the healthy plant, and the progenies of the rusted plants are again rusted, we have evidence that our assumption is correct

The environmental and heritable variations in plants are not entirely independent of each other and these two types frequently interact in their effect on the plant For example, mutant chlorophyll deficient seedlings are observed occasionally in maize in contrast to normal green seedlings But chlorophyll will not develop in the "normal" maize seedling unless the seedling is exposed to light of sufficient intensity A rust resistant variety of wheat may have no yield advantage over a rust-susceptible variety in seasons unfavourable for the development of rust Selection of individual plants of rice for tillering capacity may be misleading unless the plants are grown with comparable spacing between plants Otherwise, the thinly spaced plants will have more plant nutrients available to them and will tiller more profusely than the plants growing in more crowded conditions

In the consideration of hereditary variations within a species, we are dealing with the contrasting *forms* of specific plant characters The *characters*, or *traits*, are determined by particular *genes* on the chromosomes and the interaction of these genes with the environment The gene is the hereditary unit that is passed on from one generation to the next The hereditary variations are of major interest to the plant breeder Without them there could be no heritable plant improvements. The breeder's particular task is to sort out those heritable variations which will be useful for the improvement of crop plants and concentrate them in a variety The characteristics which he looks for are varied and often they are complex, for the economic improvement of field crops takes into consideration a wide range of plant characteristics Some improvements affect morphological or structural features of the plant, such as those related to straw stiffness Other improvements are concerned with physiological processes such as heat or drought resistance or response to fertilizer applications Still other improvements such as disease resistance relate to pathology Some characters desired by a breeder are easily identified and simply inherited Others are exceedingly complex from the standpoint of both identification and inheritance

One of the difficult problems of the breeder is to determine to what extent a characteristic is heritable and is the result of gene action, and to what extent it may be the result of favourable or unfavourable influences in the environment This distinction is usually more difficult if the variation in the character is measured by minute quantitative units, which are affected to a greater extent by changes in the environment than are the simple and qualitatively measured characteristics of a plant Yield is an example of a complex character that is measured in quantitative units As a result, the comparative yielding ability of two varieties cannot be accurately determined unless the varieties are grown in the same soil and climate, and all conditions affecting their growth are kept as nearly identical as possible If the differences observed in characteristics of plants are inherited, similar differences should be observed in succeeding generations under similar environmental conditions For this reason progeny tests are commonly conducted by plant breeders to observe the breeding behaviour of particular plants

How Heritable Variations Originate. Heritable variations in plants originate from (*a*) gene recombinations after hybridization, (*b*) mutations, and (*c*) polyploidy By these processes the plant species have evolved in nature and reached their present stage of development The breeder isolates

the plant types which fulfil his needs by selection from natural genetically mixed populations of a plant species Or he may employ the above forces to create new populations from which to select This requires a comprehensive and thorough knowledge of the mechanism of heredity and the principles upon which it operates Such a study is beyond the scope of this text, but it may be found in the many excellent textbooks on genetics It is possible here only to review some of the more pertinent genetic principles and relate them to plant breeding procedures

THE MECHANISM OF HEREDITY

The mechanism of heredity is dependent upon the behaviour of chromosomes and the genes they carry Some facts regarding characters, genes, and chromosomes are summarized here

1 A mixed population of a plant species is marked by many variations that are hereditary in nature From this assortment the breeder selects plants with *traits* or *characters* important for the development of improved varieties Examples of such traits are seed colour, seed size, plant height, earliness of flowering and maturity, leaf shape, stem size, disease or insect resistanee, and chemical constitution of the seed Heritable variations result when different plants exhibit contrasting forms of these traits or characters The contrasting traits are determined by alternative (contrasting) genes, and the interaction of the genes with the environment during the growth and development of the plant

2 The *genes* are located on the chromosomes They are the determiners of the characters of a plant The influence of each gene may be exerted individually or in combination with other genes, and *in conjunction with the environment* The action of a gene is specific for the character or characters which it influences Each gene is found in a certain position, or *locus*, on a specific chromosome and is duplicated when the chromosome divides The genes occur in alternative kinds, called *alleles*, which result in the development of contrasting forms of the characters they determine Genes that express themselves to the exclusion of their alleles are referred to as *dominant* The contrasting form of a gene, which is not expressed in the presence of the dominant, is referred to as the *recessive* Genes are commonly represented by a letter or combinations of letters, a capital for the dominant (*A*) and a small letter for the recessive (*a*) Breeding behaviour of a plant is determined by the particular combination of genes that it possesses Plants with like genes at a given locus on *homologous chromosomes* (chromosomes that pair) are *homozygous* (*AA* or *aa*) for the genes concerned Plants with unlike genes at a given locus are *heterozygous* (*Aa*) for those genes The exact genetic composition of a plant determines its genotype The appearance of the plant, i e, whether it exhibits the dominant (*A*) or the recessive (*a*) trait, determines the *phenotype* In some instances the heterozygotes (*Aa*) may be intermediate to the homozygotes (*AA* or *aa*), a condition known as *partial dominance* Genes sometimes change in nature so that they produce different forms of the character, the new form being reproduced in succeeding generations Such a change in a gene is known as a *mutation*

3 The *chromosomes* are rod or thread shaped bodies in the cell nucleus, and may be observed at the time of cell division if properly stained They are important in heredity because they carry the genes The distribution of the chromosomes and of the genes they carry to the germ cells determines the specific distribution of the genes to the progeny Chromosomes exist singly in haploid spores and gametes, in pairs in the diploid body cells, mother cells, and the fertilized egg, and in triplicate in the triploid endosperm cells The haploid diploid chromosome number is constant for any species Chromosomes divide longitudinally in mitotic divisions Homologous chromosomes separate during meiotic divisions

The simplest hereditary character is one that develops under the control of a single gene However, many characters of agronomic importance with which the plant breeder works, such as size, yielding ability, drought resistance, lodging resistance, or quality, are each influenced by numerous genes which may be scattered about on several chromosomes

Inheritance of Simple Characters. The mechanism of heredity may be illustrated most simply with a cross between two varieties which differ in a trait conditioned by a single gene It is necessary to make the cross and then to study the segregation of that character in the progenies

Since barley is a diploid species with most characters simply inherited, and since there is available information on the inheritance of a large

Fig 3 1 Head of an awned variety of barley (left) and a hooded variety (right) Hoods and awns are alternative forms of the lemma appendage on barley They are conditioned by a single pair of genes with the alleles for hoods (*KK*) dominant over the alleles for awns (*kk*)

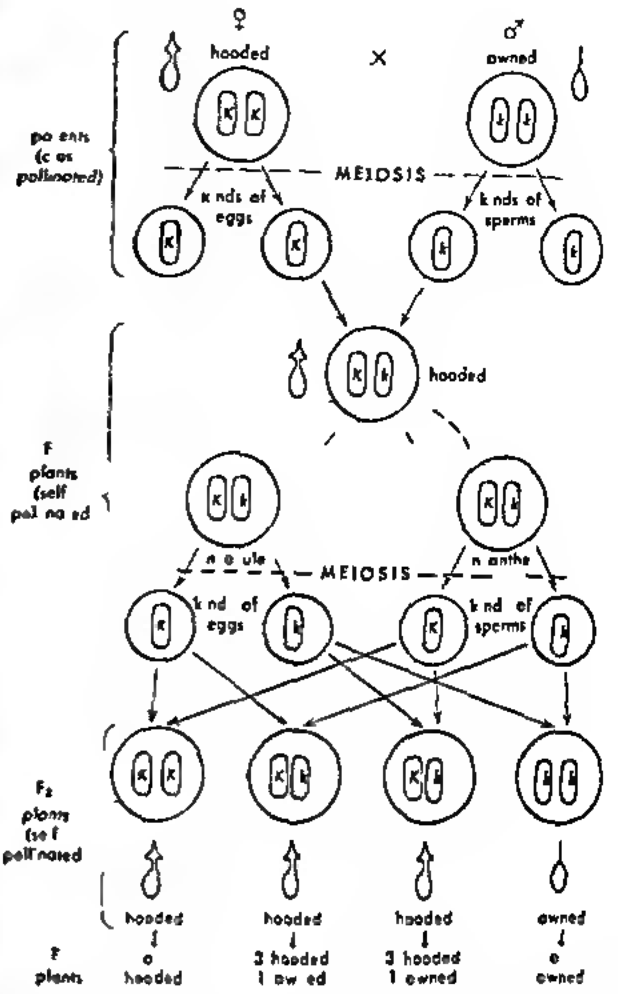


Fig 3 2 Distribution of the chromosomes carrying genes for hoods (*KK*) and awns (*kk*) in a monohybrid cross in barley In this cross hoods are dominant over awns. All F_1 plants are hooded but in the F_2 a phenotypic ratio of 3 *hooded* 1 awned is obtained

number of characters in barley, we will choose examples to illustrate inheritance from the barley crop even though barley is not an important crop economically in tropical Asia

A suitable example would be a cross between a hooded variety of barley and an awned variety (Fig 3 1) The presence of hoods is dominant to the presence of awns During meiosis the homologous chromosomes carrying the genes (*KK* in the hooded variety and *kk* in the awned variety) separate, and each germ cell (spore and egg or sperm) contains only one gene for this character (Fig 3 2) The egg and the sperm fuse with fertilization The homologous chromosomes, one containing a dominant (*K*) and one containing a recessive (*k*) gene, are brought together again within the fertilized egg The hybrid (F_1) plant that subsequently develops will be heterozygous (*Kk*) and will exhibit the dominant hooded trait Reciprocal crosses give similar results since dominant and recessive genes are brought together regardless of which variety in this cross is used as the male parent.

In the self pollinated hybrid (F_1) plant (Fig 3 2), the reduction of each mother cell results in the production of a tetrad of four spores (Fig 2 6) Two spores will contain dominant and two spores will contain recessive genes for the hood awn trait Eggs and sperms are formed from the spores after successive mitotic divisions One half of the eggs and one half of the sperms will each contain a dominant gene for hoods The remainder of the eggs and of the sperms will each contain a reces

sive gene for awns The chance fusion of the sperms and eggs will bring together dominant and recessive genes in such proportions that F_2 plants will occur in approximate ratios of 3 hooded 1 awned (Fig 3 2) This is a *phenotypic ratio*, since it is determined by the appearance of the plants The approximate ratio in which the different genotypes occur is the *genotypic ratio* This will be 1*KK* 2*Kk* 1*kk* The F_2 plants homozygous for hoods (*KK*) will produce F_3 progenies with hooded plants only The F_2 plants heterozygous for hoods (*Kk*) are like the hybrid F_1 plants and in the F_3 will produce progenies with phenotypic ratios of 3 hooded to 1 awned, or with genotypic ratios of 1*KK* 2*Kk* 1*kk* The F_2 plants homozygous for awns (*kk*) will produce F_3 progenies with awned plants only These are typical ratios that may be expected in the F_2 generation, if varieties are crossed that differ in a trait determined by a single gene A cross in which only a single pair of alleles is considered is called a *monohybrid* cross

The Progeny Test The breeding behaviour of an individual plant is learned by growing its progeny Only by this procedure can we know whether a plant is homozygous or heterozygous for a particular dominant character In the cross between hooded and awned barley, three out of each four F_2 plants were hooded To determine which hooded F_2 plant is homozygous (*KK*) and which is heterozygous (*Kk*), the seed from each is harvested and planted separately In the F_3 counts are made of the proportions of hooded and awned plants in the progeny of each F_2 plant This constitutes a progeny test Only by making the progeny test can the genotype of a specific F_2 hooded plant be identified

Progeny testing is a basic procedure in plant breeding Selection of superior plants from a mixed population is usually made on the basis of appearance or phenotype The plant breeder may select a shorter plant, a plant with more vigour, an outstanding plant that survived a severe drought or a heavy disease epidemic The progeny test provides an opportunity to evaluate the genotype of the selected plant Through its use the breeder learns whether the differences he sees are genetic and inherited, or the result of environmental variation The performance of the progeny is a better guide to the breeding behaviour of the plant than the appearance of the plant itself

HOW GENES RECOMBINE

Genes That Assort Independently. The cross between the hooded and awned varieties of barley used in the preceding illustration was greatly simplified when it was implied that these two varieties of barley differ only in the hooded awned trait Actually the varieties will differ in maturity, disease resistance, height, and in many other ways Practically all the varieties that plant breeders use in crosses will differ in many respects The usual objective of such crosses is to combine into a single plant the desirable traits of different varieties The recombination of two genes in this manner may be illustrated with a simple cross Since two pairs of alleles are considered, it is called a *dihybrid* cross

Oderbrucker was at one time a leading variety of barley in America, but it possessed an undesirable trait, barbed or rough awns The Lion variety of barley introduced into the United States from Russia in 1911 had smooth or barbless awns, but it also had black hulls which are unattractive and thus undesirable in barley From a cross between these two varieties, the Wisconsin Barbless variety was developed in which were combined the characteristics, white hulls and smooth awns Both traits, hull colour and barbing of awns, are *monogenic* (determined by single genes) The genes for the two characters are located on different pairs of chromosomes

In a dihybrid cross the distribution of the genes to the progeny will be determined by the distribution of the particular chromosomes that carry the genes During meiosis in the parent plants, the chromosome pairs separate and eventually eggs and sperms are formed which carry one member of each pair of chromosomes In the cross outlined here, the parent plants are homozygous (*BBrr* or *bbRR*), so all the gametes from a single parent will carry identical genes (*Br* or *bR*) These combine to produce heterozygous F_1 plants (*BbRr*) that will be black and rough awned in appearance (Fig 3 3)

During meiosis in the F_1 plant, the chromosome pairs separate, one chromosome from each pair moving to one pole, and the homolog moving to the opposite pole The specific chromosome of any pair which enters a particular gemete is a matter of chance Since the F_1 plant is heterozygous for two pairs of genes (*BbRr*), gametes with four possible combinations of genes will be formed in equal proportions (*BR*, *Br*, *bR*, *br*) The chance recom-

bination of the four kinds of eggs with the four kinds of sperms is shown by the checkerboard (Fig 3 3) The progeny in the F_2 generation will thus appear in the following ratios

Ratios of each character, considered separately	*Genotypes when ratios are combined*	*Phenotypes*
1*BB*	1*RR* 1*BBRR*	9*BR* black, rough awn
	2*Rr* 2*BBRr*	
	1*rr* 1*BBrr*	3*Br* black, smooth awn
2*Bb*	1*RR* 2*BbRR*	
	2*Rr* 4*BbRr*	
	1*rr* 2*Bbrr*	
1*bb*	1*RR* 1*bbRR*	3*bR* white, rough awn
	2*Rr* 2*bbRr*	
	1*rr* 1*bbrr*	1*br* white, smooth awn

It may be expected that one out of each sixteen plants in the F_2 generation will be 'white smooth awn," the combination of traits desired by the breeder in this particular cross The genotype of the "white, smooth awn' plant differs from that of either parent, hence it represents a recombination of genes

By the hybridization procedure, breeders can combine desirable characteristics of parent varieties into new types that have not been found in nature, and can thereby increase the heritable variations within that crop There are, however, limitations to the recombinations that a breeder can obtain by segregation and independent assortment Some of these are

1 *Recombinations of* genes on separate chromosomes result from the *segregation* and *recombination* of the chromosomes on which they are carried Two or more genes on the same chromosome do not assort independently, their distribution to the gametes is influenced by their linkage relations, which will be discussed in a later topic

2 In a monohybrid cross a specific homozygote may be expected in one out of each four F_2 plants, but in a dihybrid cross in which genes assort independently, the expected possibility of finding the ideal homozygous combination in an F_2 plant is one out of sixteen For crosses involving different numbers of independently assorting genes, the theoretical possibility of obtaining a particular homozygous plant will occur according to the frequencies listed below

Number of gene pairs concerned	*Expected frequency of particular homozygous type in the F_2*
1	1 out of 4
2	1 out of 16
3	1 out of 64
4	1 out of 256
5	1 out of 1,024
10	1 out of 1,048,576
20	1 out of 1,099,511,627,776

This emphasizes the need for growing an extremely large F_2 population if the breeder expects to find in the F_2 generation a plant with a specific homozygous genotype from a polyhybrid cross Actually, the possibilities are much better that the desired homozygous plant may be found in later generations, since it may arise by segregation from many heterozygous F_2 plants

Gene Interactions. While the principles of segregation and independent assortment are fundamental in genetics, yet the dihybrid F_2 ratio may not always conform to the basic 9 3 3 1 pattern due to interactions between non allelic genes Examples of some of the common types of gene interactions are listed below

1 *Complementary action* Two non allelic genes may be required to produce a single effect In Japanese varieties of rice, red pericarp (red seed coat) was controlled by two complementary genes *Rc* and *Rd* *Example* *Rc Rd**†=red, *Rc rd*, *rc Rd*, *rc rd*=white.

* *Rc* and *Rd* are each symbols for single dominant genes. The symbols for the recessive alleles are *rc* and *rd*

† *Rc Rd* as used here refers to the phenotypic designation For example a plant exhibiting dominant *Rc* may be either *Rc Rc* or *Rc rc* with respect to genotype

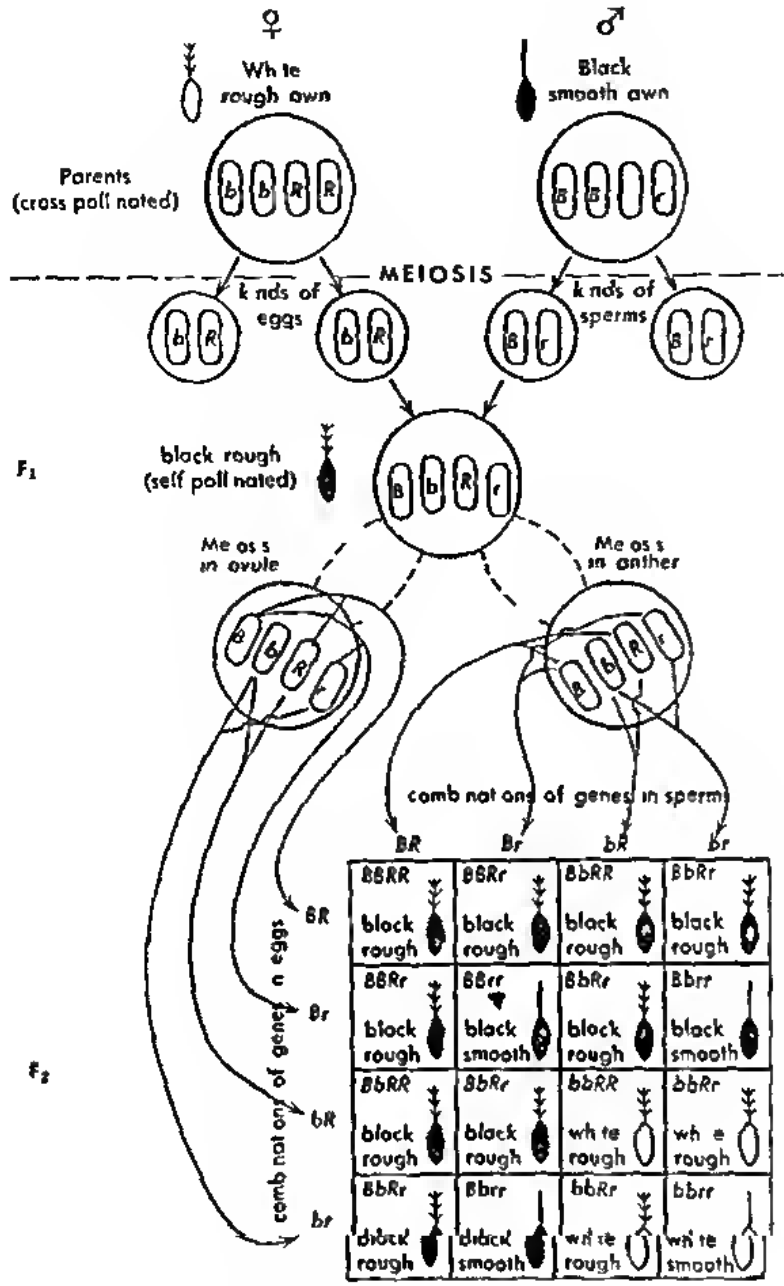


Fig 3 3 Distribution of the chromosomes carrying genes for chaff colour and barbing of awns in a dihybrid cross in barley The hybrid F_1 plant carries one set of chromosomes from the female parent and one set of chromosomes from the male parent Chromosome assortment to the eggs and to the sperms and the genes for chaff colour and barbing of awn carried by the chromosomes are shown by the arrows All possible combinations of eggs and sperms result in an F_2 phenotypic ratio of 9 black rough 3 black-smooth 3 white-rough 1 white-smooth in the F_2

2 *Modifying action* One gene may have no visible effect unless a second gene is present In maize, red colour is produced by a dominant gene *R*, the contrasting allele produces white A second dominant gene *Pr* produces purple colour in the presence of *R* but produces no effect if dominant *R* is absent *Example* *Rpr*=red, *RPr*=purple, *rpr*, *rPr*=white

3 *Inhibiting action* One gene may act as an inhibitor of the effect of another gene The dominant gene for red colour in maize, *R*, does not produce any effect in the presence of a second dominant "inhibitor" gene, *I* *Example* *RI*=red, *RI*, *rI*, *rr*= white

4 *Masking action (epistasis)* One gene may hide the effect of a second gene when both are present.

In oats, a dominant gene *Y* produces yellow seed coat colour, and a dominant gene *B* produces black seed coat colour The gene *Y* will have no visible effect in the presence of *B* since the black seed coat colour will mask the yellow colour *Example* *BY*, *By*=black, *bY*=yellow, *by*=white.

5 *Duplicate action* Either of two genes may produce a similar effect, or the same effect is produced by both of them together The floating habit of deep water rice is conditioned by duplicate recessive genes, dw_1, and dw_2 Either of the dominants will give the non floating habit *Example* Dw_1dw_2, dw_1Dw_2, or Dw_1Dw_2=non floating habit, dw_1dw_2 =floating habit

6 *Additive effect* Two genes may produce the same effect, but the effect will be intensified if both genes are present An example has been reported in barley Either *A* or *B* will produce medium length awns while the two dominant genes together produce long awns The recessive genes produce awnless plants *Example* *Ab* *aB*= medium length awns, *AB*=long awns, *ab*= awnless

If a number of pairs of genes are involved in a cross, complex interactions may further complicate the ratios *In such cases large numbers of progeny are needed to obtain a population with a proportionate representation of all classes*

Linkage. In the maize plant, which has ten pairs of chromosomes, about 500 genes have been identified (Fig 3 4) [25] Large numbers of genes have been identified in rice[5] and in many other crop species, although no plant species has been studied so extensively as maize Each chromosome is an aggregate of many genes, which tend to be inherited as a group when the chromosomes are distributed to the gametes The tendency for genes to be inherited in groups is known as linkage, and the string of genes in a chromosome is a *linkage group* The number of linkage groups in any species is equal to the number of chromosome pairs If the genes on a chromosome were so completely linked that they would not separate, there could be no recombinations between genes within the same linkage group This would impose severe restrictions on breeders, for they could not then obtain new genotypes from recombinations of linked genes Fortunately this condition does not exist Recombinations of linked genes occur as a result of a process known as *crossing over*, in which sections of homologous chromosomes are exchanged during meiosis

For a simple illustration to show how recombinations between linked genes may be obtained, let us consider a cross between two barley strains which differ in the number of rows of seed on the spike and in lemma colour In barley, the two row trait is dominant to six row, and purple lemma colour is dominant to white The genes for these two characters are located in barley Linkage Group I, with recombinations of these genes occurring 19 4 per cent of the time [16]

If two homozygous barley strains, a two row and purple strain and a six-row and white strain are crossed, the heterozygous F_1 plants will exhibit the dominant characteristics, two-row and purple (Fig 3 5) If the heterozygous F_1 plant is next test crossed to a recessive plant (six-row and white) testcross progenies are obtained in the following proportions

Genotypes[a]	*Phenotypes*	*Per cent in each class*	
$\frac{VP}{vp}$	two row, purple	40 3	*look like* parents
$\frac{vp}{vp}$	six row, white	40 3	
$\frac{Vp}{vp}$	two row, white	9 7	recombinations
$\frac{vP}{vp}$	six row, purple	9 7	

[a] $\frac{VP}{vp}$, when written in this manner, indicates that the genes above the line are linked on one chromosome, and the genes below the line are linked on the homologous chromosome

The heterozygous F_1 plant received the dominant linked genes (*VP*) in the gamete from the female parent and the recessive alleles (*vp*) in the gamete from the male parent (Fig 3 5) The paired chromosomes carrying these genes separate at

meiosis in the F_1 plant and subsequently enter separate gametes In 80 6 per cent of the F_1 gametes, the linked genes are in the same combination as they were received from the original parent plant (40 3% *VP* and 40 3% *vp*) In 19 4 per cent of the gametes, the linked genes are in new combinations (9 7% *Vp* and 9 7% *vP*) The recombinations of the linked genes occur as a result of exchange of segments of the homologous chromosomes which carry the genes (Fig 3 5) The exchange of chromosome segments is a process known as *crossing over* The percentage of recombinations for two linked genes is known as the *crossover value* For the two linked genes considered here, the crossover value is 19 4 per cent This is a specific value for these two linked genes Other linked genes will have other crossover values, depending upon the distance between the linked genes on the chromosome The greater the distance, the more frequently crossovers will occur, and the higher will be the crossover value From crossover percentages, *linkage maps*, which show the relative position of genes on the chromosomes, can be constructed for particular species (Fig 3 4)

The testcross to a recessive plant is made in the example cited (Fig 3 5) to simplify the problem In the progeny of the testcross, the ratio of phenotypes is the same as the types of gametes produced in the F_1 plants Since the breeder generally works with F_2 populations rather than testcross populations, it is of interest to study the effect of linkage on the F_2 dihybrid ratios Let us consider then what the progeny is if the F_1 plant in the above cross is self pollinated instead of testcrossed to the recessive parent

In the F_1 plant four types of gametes, both eggs and sperms, are produced (Fig 3 5) The gametes and their proportions are *VP*, 40 3%, *vp*, 40 3%, *Vp*, 9 7%, and *vP*, 9 7% The genotypes in the progeny and the proportions of each obtained when all combinations of eggs and sperms are combined are indicated in the following checkerboard.

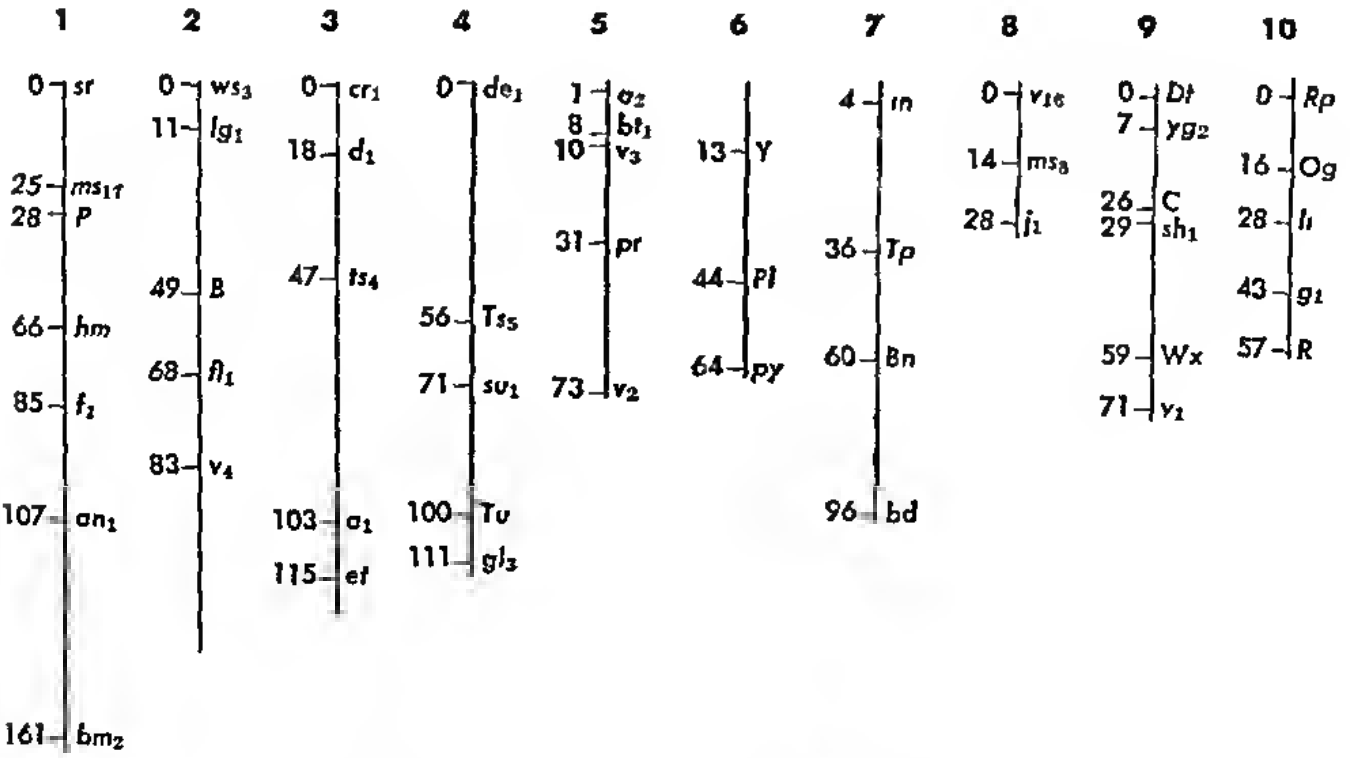


Fig 3 4 A linkage map of the ten chromosomes of maize

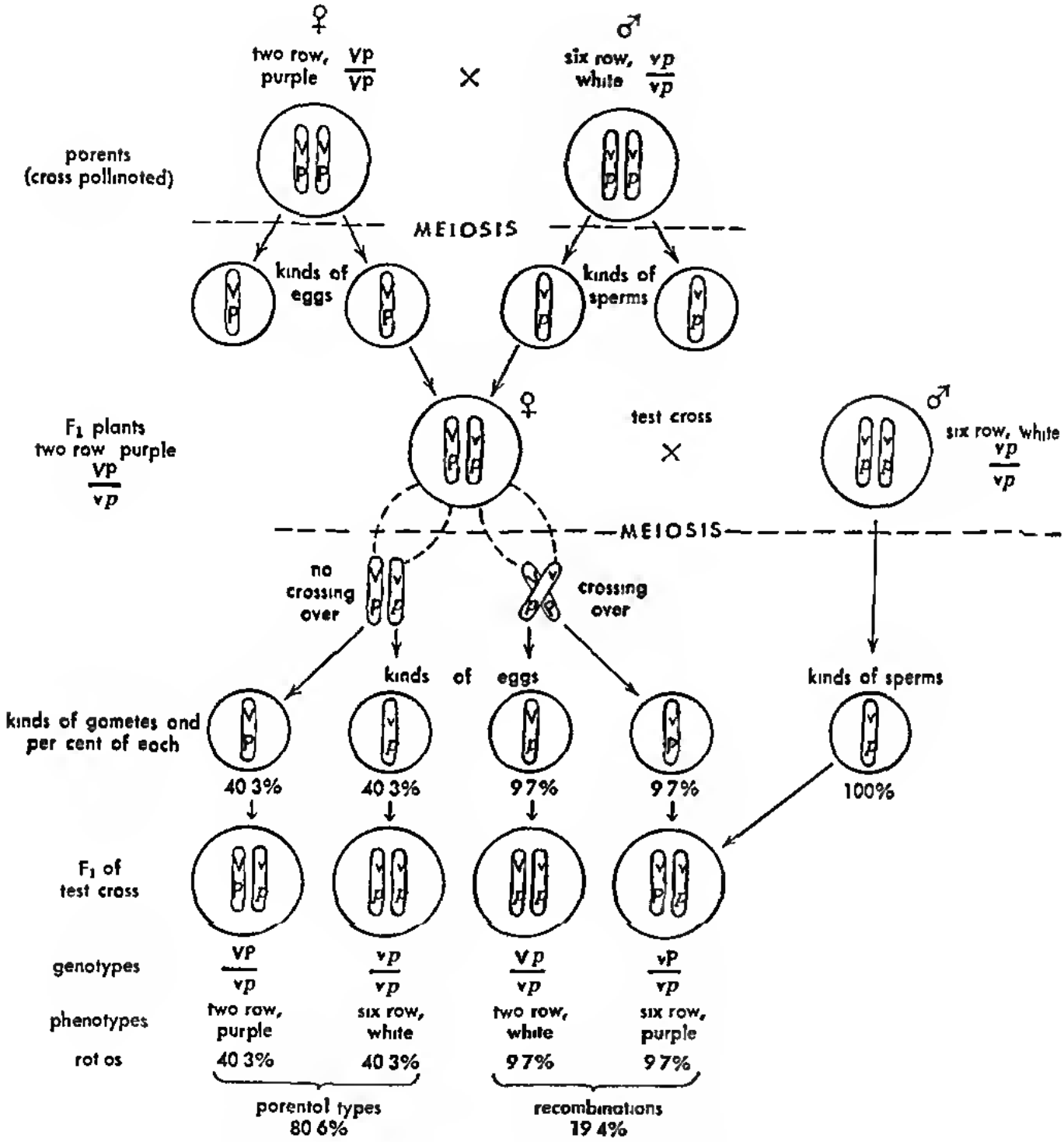


Fig 3 5 The *distribution of linked genes in a cross* In this cross a pure stram of barley containing dom nant linked genes for two row and purple seed coat characters is crossed with a pure stram containing the contrasting recessive alleles (six row and white) The heterozygous F_1 plant is test crossed to the pure recessive Four types of gametes are formed in the hybr d plant Two types of gametes have linked genes in the same combinations as received from the original parents (*VP* and *vp*) The other two types of gametes have recombinations of the linked genes (*Vp* and *vP*) which originated as a result of an exchange of chromosome segments of homologous chromosomes during meiosis The exchange of chromosome segments a process known as *crossing over*, is the means by which recombinations of linked genes occur

Eggs \ Sperms	40 3% *VP*	40 3% *vp*	9 7% *Vp*	9 7% *vP*
40 3% *VP*	16 24% $\frac{VP}{VP}$	16 24% $\frac{vp}{VP}$	3 91% $\frac{Vp}{VP}$	3 91% $\frac{vP}{VP}$
40 3% *vp*	16 24% $\frac{VP}{vp}$	16 24% $\frac{vp}{vp}$	3 91% $\frac{Vp}{vp}$	3 91% $\frac{vP}{vp}$
9 7% *Vp*	3 91% $\frac{VP}{Vp}$	3 91% $\frac{vp}{Vp}$	0 94% $\frac{Vp}{Vp}$	0 94% $\frac{vP}{Vp}$
9 7% *vP*	3 91% $\frac{VP}{vP}$	3 91% $\frac{vp}{vP}$	0 94% $\frac{Vp}{vP}$	0 94% $\frac{vP}{vP}$

The phenotypes in the progeny and the proportions of each are as follows

six row, purple (*VP*)	66 24%
six row, white (*Vp*)	8 76%
two-row, purple (vP)	8 76%
two-row, white (*vp*)	16 24%

These data show that the parental types (*VP* and *vp*) occur much more frequently than the recombinations (*Vp* and *vP*), which is a characteristic of linked genes Without linkage, a dihybrid ratio of 9*VP* 3*Vp* 3*vP* 1*vp* would have been obtained (Fig 3 3)

The principles illustrated by this example of linkage relations of genes have practical significance to the breeder in the following ways

1 Plants with recombinations of linked genes may be selected from variety crosses The percentage of recombination is fairly constant for any two linked genes

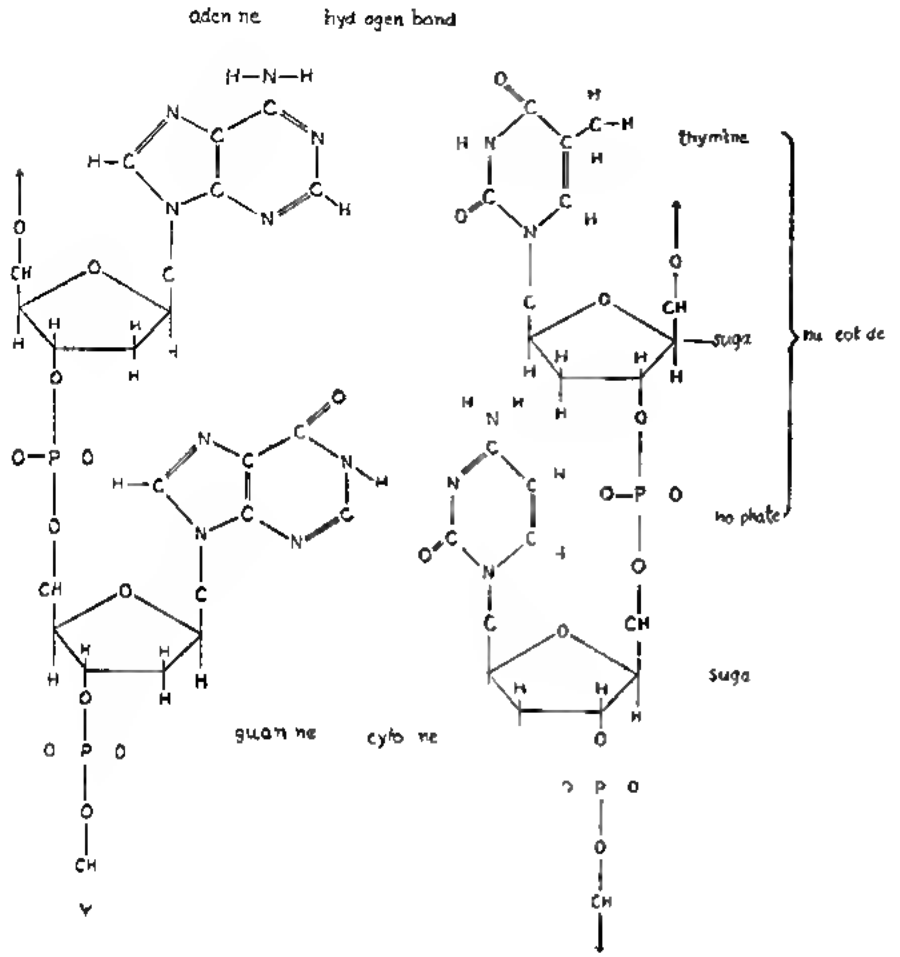
2 Since the proportion of recombinations of two linked genes will be smaller than the proportion of recombinations of two genes which assort independently, it will be necessary to grow larger F_2 progenies of crosses involving linked genes than progenies of crosses involving genes that assort independently to obtain similar numbers of recombinations The smaller the crossover value, the larger the F_2 population that will be needed

3 Linkage may be an aid to selection as illustrated by the following example Genes for resistance to two diseases in barley, stem rust and loose smut, are located in the same linkage group (Linkage Group VII) with a low crossover value [18] Inoculation techniques for identifying plants resistant to stem rust are easier to carry out than inoculation techniques for identifying plants resistant to loose smut If a parent in a barley cross contains the linked genes for resistance to both diseases, considerable selection for resistance to loose smut could be effected by the simple expedient of selecting plants in the progeny with stem rust resistance Linkage may be a handicap to the breeder if genes for good characters are linked with genes for undesirable characters

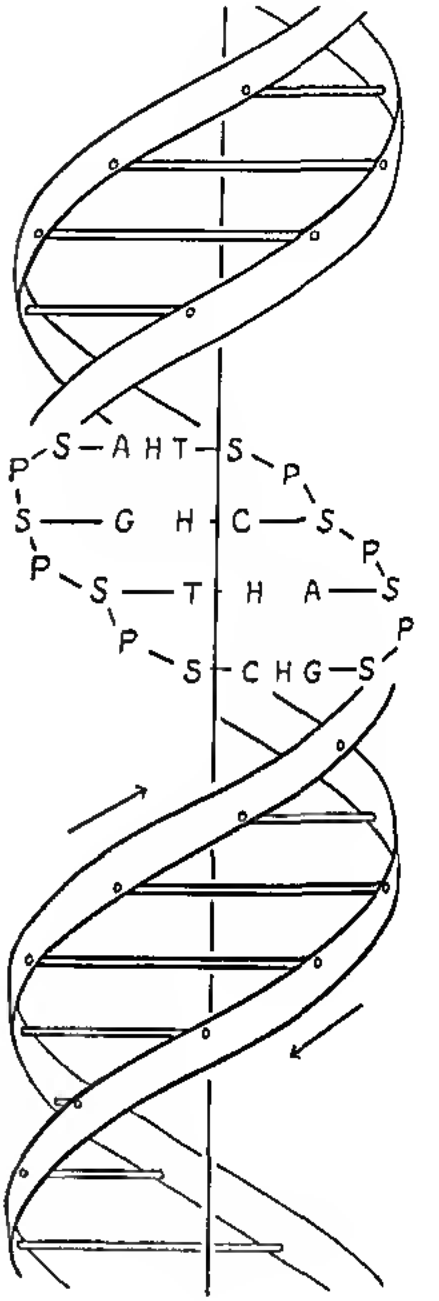
Information on crossover values permits mapping of genes on specific chromosomes (Fig 3 4)

GENE STRUCTURE AND ACTION

Thus far we have referred to the gene in the classical sense only, as a unit in the structure of the chromosome Recent researches have supported the idea that the genetic material in the higher organism is deoxyribose nucleic acid (DNA) [19] DNA is a compound of high molecular weight and is composed of nitrogen bases (purines and pyrimidines), deoxyribose, and phosphate groups The purines include adenine (*A*) and guanine (*G*) while the pyrimidines include cytosine (*C*) and thymine (*T*) When a nitrogen base is bound to a deoxyribose sugar and a phosphate group the resulting molecular structure is called a nucleotide Such nucleotides are linked together to form a polynucleotide chain in which the sugar of one nucleotide is bound to the phosphate group of another and so on According to the Watson C
of the structure of DNA, it is made up
helically coiled chains of polynucl
base pairs connected by h en
The pairing bases are always spe



3 6A



3 6B

Fig 3 6 Structural diagram of a portion of DNA A The sugar phosphate linkage between nucleotides to form a polypeptide chain B Specific pairing of nitrogen bases adenine with thymine and guanine with cytosine connected by hydrogen bonds

adenine will always pair with thymine while cytosine pairs with guanine only

A change in any of the base pairs for example from A—T to C=G will lead to a change in the DNA or gene The DNA or gene staying on the chromosome inside the nucleus controls the expression of a character through its mechanism of controlling protein synthesis The DNA specifies the synthesis of enzymes, which are also proteins, and thus controls the metabolic activities inside the plant To extremely simplify the situation we may say that a particular DNA may initiate the formation of a particular enzyme which may in turn aid the plant to synthesize a purple pigment, anthocyanin Thus the phenotypic expression of anthocyanin or purple pigmentation in the plant would be controlled by this particular DNA or gene

The studies of such biochemical or physiological genetics have greatly increased in recent years and

our knowledge of these phenomena has been greatly expanded, yet a perfect understanding of the whole situation is still awaited Neither do we have a clear picture as to how this information can be utilized by the plant breeder Should it become possible to control specific changes in the gene material, which in turn would produce specific changes in chemical reactions, and in the plant's metabolism, we would have a powerful tool for the use of the plant breeder

QUANTITATIVE INHERITANCE

The examples of inheritance that we have considered thus far have dealt with traits that are simply inherited, mostly by single genes With respect to any one of these traits, the phenotypes can be classed into a small number of easily recognized, qualitative groups For example, a barley plant may have black or white hulls, two or six rows, rough or smooth awns, or rust resistance or rust susceptibility But many of the traits of agronomic importance with which the breeder works are not inherited in this simple manner One of these traits is yielding ability If a large number of strains of a particular crop were selected at random from a mixed population, they could not be classed into the two specific groups, high yielding ability or low yielding ability Instead, the strains would differ in yield by rather minute amounts and would range rather uniformly from high to low in yielding ability If the strains were classed according to their relative yielding ability into small groups, the groups would tend to fit into the pattern of a normal curve Characters of this nature that show a continuous range of variability from one extreme to the other are referred to as *quantitative characters* Their inheritance is dependent upon many genes, each of which contributes in an additive manner to the final effect Typical quantitative characters are more influenced by the environment than are qualitative characters

The classic study of quantitative inheritance is an experiment dealing with colour of wheat It was reported by a Swedish geneticist and plant breeder, Nilsson Ehle, in 1908 In one experiment, two varieties of wheat, one with very dark red kernels and one with white kernels, were crossed The F_1 produced kernels that were intermediate in colour In the F_2, the colour ranged from very dark red to white This was explained on the basis of two pairs of genes with each individual dominant gene adding to the intensity of the red colour This is illustrated in the following table

Parents	*Very dark red* $R_1R_1R_2R_2$	×	*White* $r_1r_1r_2r_2$
F_1		*Medium red* $R_1r_1R_2r_2$	

F_2 *genotypes*	*Colour*	*Number of dominant genes*	*Number of plants in* 16
$1R_1R_1R_2R_2$	very dark red	4	1
$2R_1R_1R_2r_2$ $2R_1r_1R_2R_2$	dark red	3	4
$1R_1R_1r_2r_2$ $4R_1r_1R_2r_2$ $1r_1r_1R_2R_2$	medium red	2	6
$2R_1r_1r_2r_2$ $2r_1r_1R_2r_2$	light red	1	4
$1r_1r_1r_2r_2$	white	0	1

In the cross given in the table, one out of each sixteen F_2 plants was as extreme as a particular parent in colour The other genotypes were intermediate to the parents in colour The distribution of the F_2 plants into colour classes, according to the number of dominant genes, illustrates the effect of individual genes on the continuous variation exhibited in quantitative inheritance Since only two pairs of genes were involved in this cross, a particular parent type may be recovered easily (one plant out of sixteen) However, if the number of genes concerned should be large, a huge population might need to be grown to have a good mathematical chance of recovering the parental types

Another consideration in the inheritance of quantitative characters is that some of the progeny may fall outside of the range of the parents

Consider next the example of a cross between two varieties of wheat, each with medium red kernels

Parents	*Medium red* $R_1R_1r_2r_2$	×	*Medium red* $r_1r_1R_2R_2$
F_1		*Medium red* $R_1r_1R_2r_2$	

F_2 *genotypes*	*Colour*	*Number of dominant genes*	*Number of plants in* 16
$1R_1R_1R_2R_2$	very dark red	4	1
$2R_1R_1R_2r_2$ $2R_1r_1R_2R_2$	dark red	3	4
$1R_1R_1r_2r_2$ $4R_1r_1R_2r_2$ $1r_1r_1R_2R_2$	medium red	2	6
$2R_1r_1r_2r_2$ $2r_1r_1R_2r_2$	light red	1	4
$1r_1r_1r_2r_2$	white	0	1

In the cross given in this table, kernels darker in colour and kernels lighter in colour than the parent varieties are obtained in the F_2 generation Plants with traits which arise by segregation outside the range of the parents are known as *transgressive segregates* Transgressive segregation occurs when the parents are intermediate to the extremes of the segregating population This principle is used extensively by breeders to obtain segregates superior to the parental types for traits inherited in a quantitative manner For example, in a cross between two high-yielding varieties, each of which possesses a different combination of genes for yielding ability, plants may be selected from the progeny with a combination of genes for yielding ability more favourable than that contained in either parent Likewise, plants may be selected with a combination of genes for yield inferior to those contained in either parent

In the example of quantitative inheritance cited here, colour of wheat was explained on the basis of multiple genes which (*a*) produce equal effects, (*b*) are cumulative in their total effect, and (*c*) do not exhibit dominance between alleles Although this was an early concept of quantitative inheritance, it would be a gross oversimplification to assume that all quantitative characters are inherited in so simple a manner Some characteristics of a quantitative nature, such as yielding ability, are influenced by so many vital processes within the plant and by the reaction of these processes to the environment that their inheritance will be much more complex Some genes that influence yielding ability may have greater effects than others Genes may also differ in degree of dominance One thing is certain—that yielding ability is influenced by the cumulative effect of all the genes

Many traits important in the breeding of crop plants are quantitative in nature In addition to yielding ability, these include size, winter hardiness, resistance to lodging, kernelweight, and quality Many of these traits are so complex that they should be partitioned into simpler components and each of the components studied separately This would facilitate the evaluation of quantitative characters in breeding and genetic studies Although many attempts to separate these complex characters into simpler components have been made, very few have been successful

Most characteristics of agronomic importance that are inherited in a quantitative manner will be determined by many more genes than determine colour of wheat, the example cited here With a large number of segregating genes, as in wide variety crosses, it is rarely possible or feasible to grow a large enough population to recover all the possible segregates in the F_2 generation But neither is this necessary, since many potential desirable genotypes can be obtained in later generations as a result of segregation and recombination (Fig 3 7)

Formulas have been proposed for estimating the number of genes involved in the inheritance of a quantitative character But with most crosses made for breeding purposes, it is usually impractical to

make the detailed measurements necessary for calculating the number of genes Often the best the breeder can do is to estimate if the character is governed by a large number or a relatively few genes Some estimate may be made from the similarity of the parent varieties Parents that are similar in appearance and breeding, with respect to the quantitative character under consideration, will probably differ by fewer pairs of genes than if the parents are dissimilar in appearance and

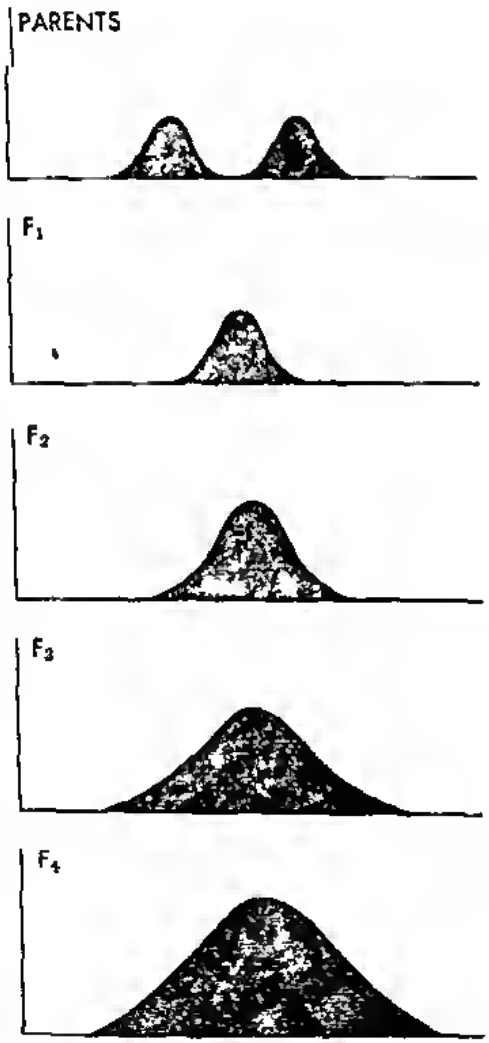


Fig 3 7 Transgressive segregation in a cross The parent varieties are populations which differ widely in a quantitative characteristic The F_1 generation is intermediate to the parents If a large number of genes is involved as with many *agronomic characteristics* inherited in a quantitative manner, the potential range of segregation is not reached in the F_2 but will broaden in succeeding generations as a result of segregation and recombination

breeding The plant breeder may find it easi select a desirable type if the parent varietie not differ too greatly in genotype so that genes and less segregation is involved, and assumed that both parent varieties are re satisfactory already On the other hand, there be greater possibilities of obtaining the rare *greatly superior segregate* from crosses betw plants with more diverse genotypes

HERITABILITY

Individual plants in a mixed population vary in yield, height, winter hardiness, or characteristics of a quantitative nature If *plants are selected at random from a mixed p* lation and their yields are measured, the diff in the yields of the two plants will be due in p to the effects of heredity and in part to the effect of environment One of the two plants may b inherently more productive, but if it is grown o *less fertile soil, its measured yield may barel* exceed, or may be even less than, the yield of th second plant If the first plant is grown on mor fertile soil, its apparent yield superiority over th second plant may be accentuated The effective ness of selecting for plants with high yield within a mixed population will depend (*a*) upon the extent to which the variability in yield in the population is the result of genetic factors and is thus transmitted to the progenies of the selected plants and (*b*) upon how much the variability in yield is due to the environment in which the plants are growing Selection of plants for yield would be ineffective if the *environmental variation is so* great that it masks the genetic variation The degree to which the *variability of a quantitative character* may be transmitted to the progeny is referred to as *heritability Heritability* may also be defined as the proportion of the total variation in a progeny that is a result of genetic factors and may be transmitted If, in a progeny, variation due to environment is large in relation to the heritable variations, then heritability will be low If variation due to environment is small in relation to the heritable variation, then heritability will be high

Heritability Estimates. Various methods have been developed for estimating heritability using statistics as the tool[1-4] These methods are based on partitioning the total biological variation of a population into the genetically controlled and

G

nvironmentally controlled components The
r next tic that is most important here is the *variance*
, of wh which is the average of the squared devia-
²) of the individual observations from a
This is calculated from the formula

$$V=\frac{d^2}{n-1}$$

e V is the variance, d^2 is the sum of the squared
itions, and n is the number of observations
are determining the variance for a character
types eight in an F_2 population, the height of
individual F_2 plant would be measured and,
n the deviations of the height of the individual
nts from the mean height of the F_2 population,
variance may be calculated

The variance calculated in the example just described would include the total variation in height from all causes While some plants would be taller or shorter than others due to genetic differences, height of the plants would also be affected by environmental factors such as spacing, soil fertility or moisture differences The total variation may be described statistically as the *phenotypic variance* (V_P) The phenotypic variance may in turn be divided into two components, *genetic variance* (V_G) and non-genetic or *environmental variance* (V_E) It follows then that

$$V_P=V_G+V_E$$

In breeding and genetic experiments, especially those concerned with quantitative characters, where genetic differences in the trait being measured may be small and where the trait may be easily altered by differences in the environment, it is essential that the experiment be conducted under conditions which will minimize the effect of the environment Therefore, if the breeder is interested in selecting for height differences in an F_2 population, the F_2 plants should be grown in a uniform soil area, with all plants receiving uniform spacing, fertilization and cultural treatments

One way the amount of environmental variation may be measured is to grow a population which does not have genetic variation, such as in the vegetative offspring from a single plant (clone), or in the self-fertilized progeny from a homozygous plant, or in the F_1 generation from a cross between two homozygous plants Since V_G would equal zero in such a population, then V_P would equal V_E When an F_2 population is being grown, a fairly accurate approximation of V_E may be obtained by growing the parents and an F_1 population under similar conditions An average of the V_P for the two parents, or for the two parents and the F_1, would then be used as an estimate of V_E viz

$$V_E=\frac{V_{P_1}+V_{P_2}}{2} \text{ or } V_E=\frac{V_{P_1}+V_{P_2}+V_{F_1}}{3}$$

We have defined heritability (H) as the proportion of the total variation that is due to genetic causes Thus

$$H=\frac{V_G}{V_P} \text{ or } \frac{V_G}{V_G+V_E}$$

The genetic variance (V_G) is composed of three major components, (*a*) *additive genetic variance* (V_A), (*b*) *dominance deviations* (V_D) and (*c*) *non allelic interactions* or *epistasis* (V_I) This may be written as

$$V_G=V_A+V_D+V_I$$

Additive genetic variance is the variance contributed by alleles having linear quantitative effects The resemblance between parents and offspring is largely the result of additive genetic variance *Dominance deviation* is deviation from the additive variance that arises when the heterozygote is more like one homozygote than the other Statistically the dominance component represents the deviation of the heterozygote from the mid point or average of the homozygous parents The dominance deviations are generally small in comparison with additive variance *Non allelic gene interactions* or *epistasis* result from interactions between additive components, interactions between dominance components, and interactions between additive and dominance components The magnitude and role of non allelic interactions are difficult to evaluate but it is generally believed that they are small in comparison with additive and dominance variations and are often ignored in calculating heritability estimates

3 10A

3 10B

3 10C

Fig 3 10 Mutation induced by irradiation Many irradiation induced mutations are curios ities such as these and have no value to the plant breeder A Red petal spot in cotton B Rugose plant type in soybeans The leaves are wrinkled and dark green in colour C Compacto d (left) and spelto d mutant in wheat

Swedish workers later isolated useful mutants from other agricultural crops[8 9] Their findings stimu lated much interest among breeders in the possi bilities of inducing useful mutations in crop plants by subjecting plants or seeds to ionizing radiations This system of breeding has since been designated *mutation breeding*

Although mutation breeding offers intriguing possibilities for finding a new trait such as resist ance to some virulent race of rust for which the breeder has no known genes available its use has some limitations some of which may be listed

1 Most mutations that occur are undesirable and have no value to the breeder Many of them are lethal

2 The mutation rate is at best very low, and very large numbers of plants must be examined to find desirable mutants

3 The stability of a mutant strain must be carefully tested

4 An early belief that the breeder may improve one or two weak characteristics while maintaining the identity and performance of a variety in all other respects may need to be changed For ex ample, a mutation for shorter straw or earlier

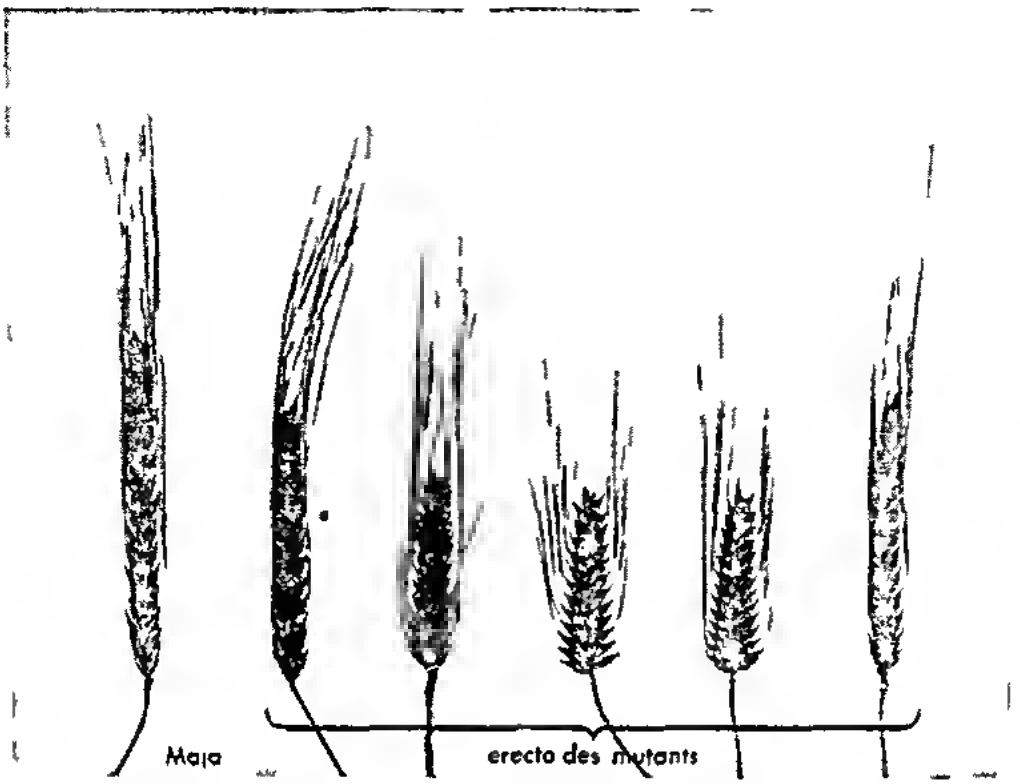


Fig 3 11 Erectoides mutations in barley Maja the mother strain is at left and five mutant strains at right The erectoides (dense head) character is associated with short stiff straw

maturity in a variety of rice may change the physiology of the plant to such an extent that it will no longer be as productive as before

5 The minute micromutations which in the long run may be more useful to the plant breeder, as they do not unbalance the genotype as drasti cally as do the striking large or macromutations, are usually difficult to identify and measure

Evidence indicates that radiation induced muta tions may be losses of chromosomal material in which valuable genes as well as undesirable ones are lost Mutation breeding is still in the develop mental stages Much additional information must be obtained before the exact relation of this new method to the more conventional methods of plant breeding is well established With the wide current interest in mutation breeding and the extent of the work currently in progress additional in- formation is rapidly being accumulated

In addition to the use of x ray and other radia tions to induce mutations in plants, *x rays have been used to effect gene substitution from alien chromo somes* [17] This procedure involves interspecific cross ing, and will be discussed later in this chapter The use of mutation breeding as a tool of the plant breeder will be discussed in the next chapter on "Methods of Breeding Field Crops" and in some of the chapters dealing with specific crops

POLYPLOIDY AND PLANT BREEDING

Polyploidy is a condition in which individuals have more than *two chromosome sets, or genomes* in their somatic cells In contrast to the normal diploid ($2n$), they may be triploid ($3n$), tetraploid ($4n$), pentaploid ($5n$) hexaploid ($6n$), and so on (Fig 3 13) Polyploid plants may arise by duplication of the chromosome sets from a single species, *autopolyploidy*, or by combining chromosome sets from two or more species, *allopolyploidy* (Fig 3 14) Allopolyploidy is the more common method of ploidy in nature An allopolyploid in which the total chromosome complement of two other species is combined to form a fertile species hybrid, is referred to as an amphidiploid Many commonly cultivated crop species have evolved in nature as polyploids Some groups of closely related species of crop plants which may be arrayed in polyloid series are listed here

Species	*Common name*	*Somatic (2n) chromosome number*
Avena strigosa	sand oats	14
Avena barbata	slender wild oats	28
Avena sativa	cultivated oats	42
Gossypium arboreum	cultivated Asiatic cotton	26
Gossypium thurberi	wild American cotton	26
Gossypium hirsutum	American upland cotton	52
Gossypium barbadense	sea island and American Egyptian cotton	52
Nicotiana sylvestris	wild tobacco	24
Nicotiana tabacum	tobacco	48
Sorghum versicolor	wild grass sorghum	10
Sorghum vulgare	sorghum	20
Sorghum halepense	johnsongrass	40
Triticum monococcum	einkorn	14
Triticum dicoccum	emmer	28
Triticum aestivum	common wheat	42

Other examples of polyploids will be cited in the chapters concerning the breeding of individual crop plants

The origin of the genomes and the exact chromosome homology is known only for a relatively few polyploid species Common wheat (*Triticum aestivum*) American Upland cotton (*Gossypium hirsutum*), various species of cultivated and wild tobacco (*Nicotiana*), and various species of rape (*Brassica*) are perhaps the best examples from crop plants

The naturally occurring polyploid relationship found in the *Brassica* species is interesting and will be related here in detail [24] Three common diploid species of *Brassica B campestris, B nigra* and *B oleracea* have haploid chromosome numbers of 10, 8, and 9, respectively These have been assigned

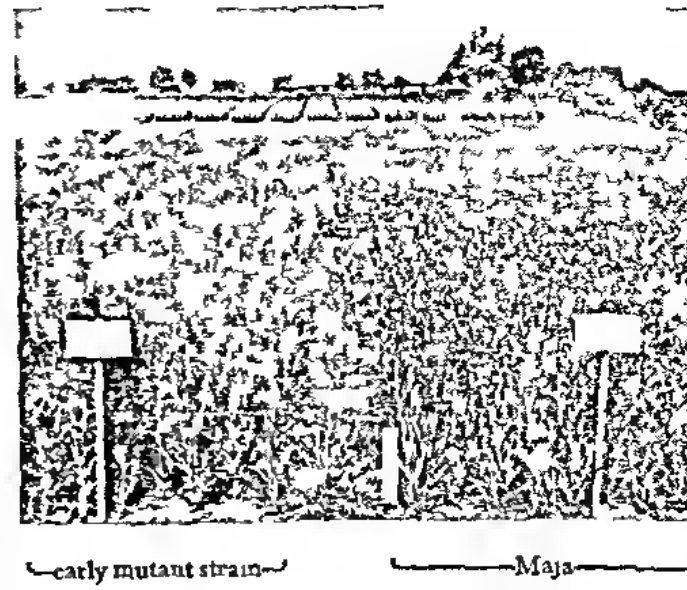


Fig 3 12 Mutation for early maturity in barley The early mutant strain is compared here with Maja the mother strain

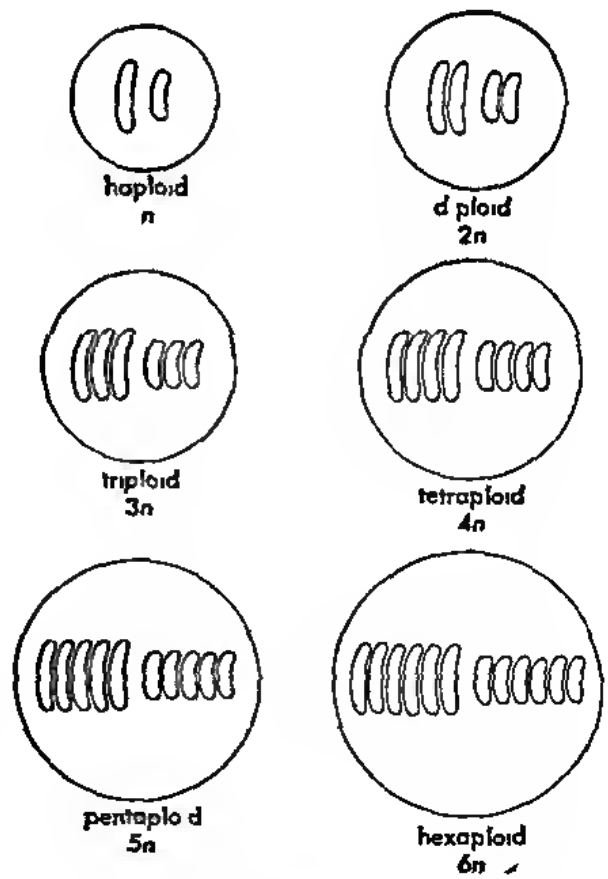


Fig 3 13 Condition

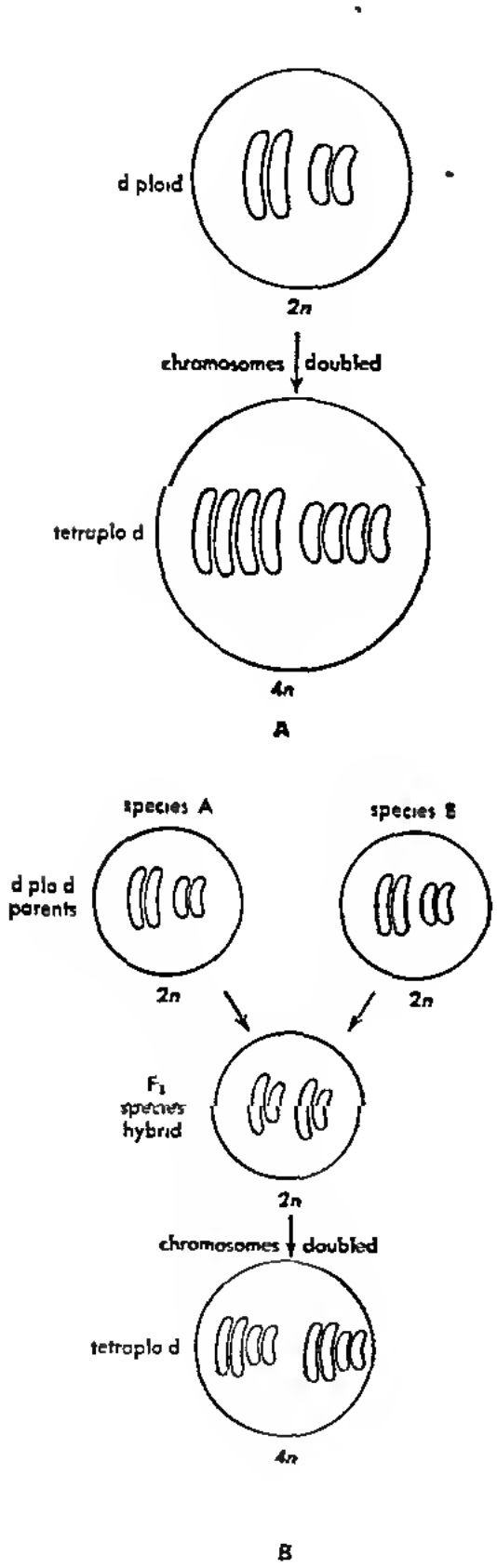


Fig 3 14 Origin of polyploids A *Autopolyploids* arise by duplication of chromosome sets in a single species B *Allopolyploids* arise by combining sets from two or more species

the genomes designations *A*, *B*, and *C* (Fig 3 15) *B juncea* (*AABB*) is a natural amphidiploid combining the genomes of the two species, *B campestris* (*AA*) and *B nigra* (*BB*) *B napus* (*AACC*) is a natural amphidiploid combining the genomes of the two species, *B campestris* (*AA*) and *B oleracea* (*CC*) *B carinata* (*BBCC*) is a natural amphidiploid combining the genomes of the two species, *B nigra* (*BB*) and *B oleracea* (*CC*) This relationship is shown by the accompanying table and is discussed further in Chapter 17 on breeding oilseed crops

Species	*Common name*	*Somatic chromosome number*	*Genome formula*
	DIPLOID SPECIES		
Brassica campestris	turnip rape	20	AA
Brassica nigra	mustard, black	16	BB
Brassica oleracea	cabbage, broccoli, etc.	18	CC
	TETRAPLOID SPECIES		
Brassica juncea	mustard, India or curled	36	AABB
Brassica napus	rape	38	AACC
Brassica carinata	mustard, Abyssinian	34	BBCC

The origin of the tetraploid species is demonstrated experimentally by crossing the diploid species in question, doubling the chromosome number of the hybrid plant, and then crossing the experimentally produced amphidiploid with the tetraploid species having a corresponding chromosome number The homology of the chromosomes is verified by the extent to which they pair and form bivalents at meiosis, and by the observed fertility of the hybrid plant.

Another amphidiploid that has received considerable attention by plant breeders is the rye-wheat hybrid, also known as *Triticale*[13, 14] This involves a cross between species of two different

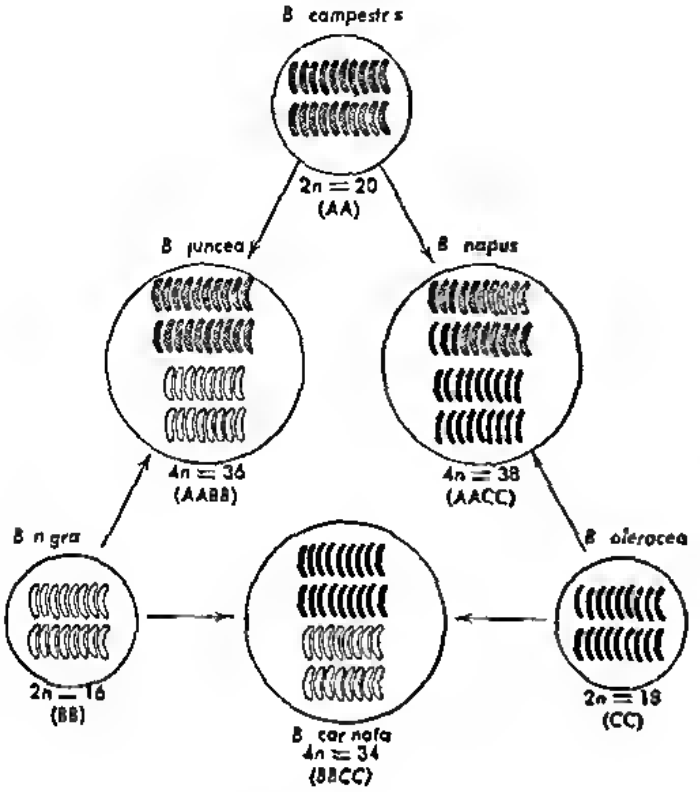


Fig 3 15 Polyploidy in *Brassica* The diploid species, *B campestris*, *B nigra*, and *B oleracea*, have chromosome numbers of $2n = 20$, $2n = 16$, and $2n = 18$, respectively, to which have been assigned the genome designations of *AA*, *BB*, and *CC* The tetraploid species, *B juncea*, *B napus* and *B carinata*, are amphidiploids, and originated by combinations of diploid species as illustrated in this diagram

genera, *Secale cereale* ($2n=14$) and *Triticum vulgare* ($2n=42$) The amphidiploid produced has 56 chromosomes in the somatic cells *Triticale* differs from the tetraploid species in *Brassica* in being an artificially induced amphidiploid that does not occur in nature Amphidiploids which occur in nature generally have a high degree of fertility, otherwise they would not have survived as a species Artificially induced amphidiploids may vary considerably in fertility, ranging from almost complete fertility down to complete sterility In amphidiploids, genomes from two separate species are combined within the single nucleus During meiosis, irregularities commonly arise in pairing and distribution of the chromosomes These chromosome irregularities account for the lack of fertility often experienced in species hybrids

Autopolyploids, which are produced by doubling the individual chromosomes within a plant, also hold considerable interest for the plant breeder Potato is a naturally occurring autopolyploid, but autopolyploids in nature are relatively rare Generally, autopolyploids are stockier and more vigorous than the diploids from which they were derived and tend to have larger leaves, darker green colour, larger flowers and seed, and larger cells and nuclei Autopolyploid tomatoes and yellow maize produce more vitamin C than the diploids from which they originated Autopolyploids have reduced fertility and produce fewer seeds than do the corresponding diploids Autopolyploidy is less common in nature than amphipolyploidy

Autopolyploids of soybeans, rice, barley, flax, rye, clovers, sugar beets, and other crops have been produced experimentally by doubling the chromosomes of diploid species The tendency for autopolyploids to have greater vegetative growth and reduced seed production suggests that autopolyploidy would be more useful in breeding crops harvested for their vegetative parts or for roots than for crops harvested for seed (Fig 3 16) As a result, autopolyploidy has been viewed with most interest by the breeders of forage crops, sugar beets, and similar crops harvested for their vegetative parts, as a means of obtaining plants with higher yield Autopolyploidy has been used also in the breeding of certain vegetables and flowers But autopolyploidy has not been limited entirely to the production of new varieties of crops used only for their vegetative parts or flowers Tetraploid varieties of rye have been developed which are grown commercially. In the commerc ' tetraploid varieties of rye, ' fertility

more than counterbalanced by increased seed size, so that seed yields are higher than from diploid varieties

The interest in polyploidy as a tool of the breeder was given a tremendous boost when it was discovered that *colchicine*, an alkaloid extracted from seeds or corms of the autumn crocus, *Colchicum autumnale*, could be used to double the chromosome number Colchicine acts in the production of polyploidy by arresting the development of the spindle fibres and the cell walls but it does not prevent the division of the chromosomes As a result the chromosome number is increased from the diploid to the tetraploid yet all the chromosomes remain within a single cell Several methods may be used in applying colchicine These include application of the colchicine to the seed, to young seedling plants, or to growing points such as shoots or buds

Polyploidy is of special significance in plant breeding because it adds to the genetic diversity in the plant kingdom Polyploidy offers the breeder an opportunity to bring about changes in the character of a plant by altering the chromosome number and consequently the number of genes within a single cell The effects are varied and not always favourable Reduced fertility, already discussed, is an unfavourable effect of polyploidy

Another consequence of polyploidy is to increase the complexity of genetic ratios In polyploid species, genes frequently occur in multiples of the basic chromosome number In common wheat, a hexaploid which originated from a combination of the chromosomes from three different species, many characters have been reported to be determined by three independent genes In a polyploid species, recessive plants appear much less frequently in a population than they would in a diploid species This requires that the breeder grow a much larger population of a polyploid to recover a corresponding number of recessive phenotypes than would be necessary with an ordinary diploid On the other hand, recessive mutations that are deleterious to the parent may be covered up by their dominant alleles to a greater extent in polyploids, so that they are not expressed as frequently in the phenotype of the plant

Polyploidy has been an important factor in the evolution of plant species A knowledge of its mechanics is important in understanding the relationships between certain plant species The chromosome relationships in the various species of *Brassica* have been cited as an example The genetic origins of common wheat, tobacco, cotton, and other crops have been traced in a similar manner A knowledge of these genetic relationships is useful to the breeder in planning crosses between species or between genera Interspecific crosses of this nature have been used many times to add genes for disease resistance or other characters from a wild species to a closely related cultivated species From a three way interspecific cross with cotton (*Gossypium arboreum* × *G thurberi*) × *G hirsutum*, greater lint strength was obtained, the genes for lint strength apparently coming from the wild American diploid species[3] This is of unusual interest since the wild American species is devoid of lint Genes for resistance to various diseases have been added to wheat, tobacco, and other

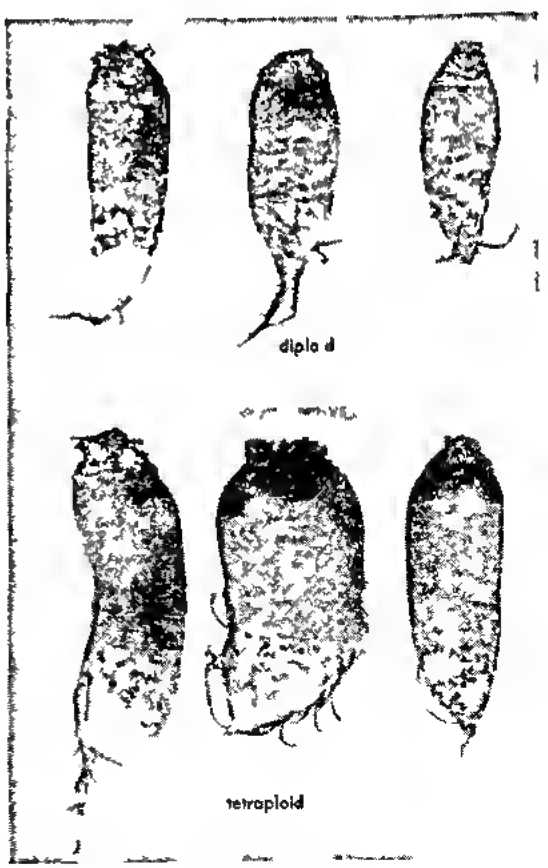


Fig 3 16 Diploid and tetraploid turnip roots Crops grown for vegetative parts usually respond more favourably to polyploidy than crops grown for seed

crops from closely related species Chromosome doubling is frequently necessary, either in one of the parent species before the cross is made or in the hybrid plant, to obtain fertile progenies from interspecific crosses

The use of polyploidy as a tool of the plant breeder will be discussed in the chapter on "Methods in Breeding Field Crops" Some polyploid relationships of specific crop species will be discussed in more detail in the chapters dealing with those crops

STERILITY AND INCOMPATIBILITY

The extent to which a crop species will set seed is an important problem with which the plant breeder must deal Either failure to be self-fertile or failure to be cross fertile may be involved Normally self pollinated species, such as rice, wheat, oats, barley, linseed, and soybeans, and some normally cross pollinated species, such as maize, usually set seed freely after self pollination or after cross pollination between varieties within the species Some self pollinated species such as tobacco and potato, and many cross pollinated species, such as mustard, rape, lucerne, rye, sugar beets, and certain perennial grasses, vary in their ability to set seed after self pollination, although they usually set seed freely after cross pollination with other strains within the species

In addition to the problem of ability to set seed after self- and cross pollination within the species, the plant breeder is also concerned about the extent to which seed may be obtained from crosses between closely related species or closely related genera The latter problem is important to the breeder as it will determine the extent to which he may be able to obtain recombinations of desirable genes from closely related species

Sterility. Sterility often results with crosses between different species or genera In this case the sterility results because the chromosomes from the two species or genera differ so greatly in genic content that they cannot pair or function normally If the chromosome difference between the species being crossed is too great, the embryo will not develop after cross fertilization of the species In more closely related species, the embryo and seed may develop, but the hybrid plant growing from them may be sterile and fail to set seed In crosses between closely related species, with similar chromosome content, the hybrid plant may be fully fertile Fertility may be restored in some species crosses by doubling the chromosomes in the hybrid plant and thus producing an amphidiploid Fertility is usually reduced in autopolyploids, after artificial doubling of the chromosome number in a species Some of the problems in interspecific hybridization will be discussed later in this chapter

The term sterility is also applied to those cases in which the inability to obtain seed set results from failure of the pollen or ovules to function normally[6] Any abnormal or imperfect development of the reproductive parts may cause sterility For example, the stamen or style may be malformed, the pollen may be defective, or the ovules may be aborted Any of these defects could result in failure to obtain seed set after either self pollination or cross pollination

Incompatibility Incompatibility is the failure of plants with normal pollen and ovules to set seed due to some physiological hindrance which prevents fertilization[6] A common cause of incompatibility is the failure of the pollen tubes to grow down the styles so that fertilization may occur In incompatible matings the pollen tube grows so slowly that it may never reach the ovule, or if it does, the ovule will already have withered In compatible matings of the same species, the pollen tube grows at a normal rate and fertilization occurs after the tip of the pollen tube enters the ovule The rate of pollen tube growth is controlled by a series of alleles (S_1, S_2, S_3, etc) for incompatibility If the allele present in the pollen tube is identical with an allele in the stylar tissue, the pollen tube normally grows at a very slow rate If the allele in the pollen tube differs from the alleles in the stylar tissue (the stylar tissue is diploid), the pollen tube grows at the normal rate. If a plant with the genotype S_1S_2 is pollinated with its own pollen, or with pollen from another plant with the S_1S_2 genotype, the pollen tubes rarely penetrate the style far enough to reach the ovule (Fig 3 17A) If a plant with the S_1S_2 genotype is pollinated with pollen from a plant with genotype S_1S_3, normally only the pollen with the S_3 allele will penetrate the style and fertilize the ovule (Fig 3 17B) If the S_1S_2 genotype is pollinated with pollen from an S_3S_4 plant, either the S_4 pollen or the S_4 pollen may

fertilization (Fig 3 17C) However, the effect of the alleles is not so great as to prohibit self-fertilization entirely, for an occasional seed may set from pollen carrying the same allele as the stylar tissue Also in some species, self-fertility alleles (*Sf*) have been found which render the alleles for incompatibility ineffective Since the incompatibility allele in the style opposes the penetration of pollen tubes with like genes, this explanation of incompatibility was called the "oppositional factor hypothesis" by East and Mangelsdorf, who used it to explain results observed in tobacco (*Nicotiana*) The genetics of incompatibility has since been worked out for several species of *Trifolium* Other crops which may set a low percentage of seed after self-fertilization include rye, sugar beets, some perennial grasses, sweetclover, lucerne, and mustard

MALE STERILITY AND ITS UTILIZATION

In many crops, plants have been observed in which the male reproductive organs are maldeveloped or aborted so that no viable pollen will be formed This condition is known as male sterility and may be inherited due either to genetic or to cytoplasmic causes

The success of the modern method of breeding hybrid maize prompted the utilization of hybrid vigour in the breeding of other crops But the necessity in many crops of making the crosses by laborious hand procedures prevented wide adoption of the method The procedure of making hybrids is greatly facilitated now in certain crops by the utilization of male-sterile lines This eliminates the tedious emasculation process in sorghum, bajra, wheat, onions, and sugar beets, and the detasseling process in maize In male-sterile lines the flowers do not produce functional anthers, and hence can not self pollinate If a male-sterile line is grown in isolation with a normal line, seed produced on the male sterile plants will then have resulted from cross-pollination with the normal Male

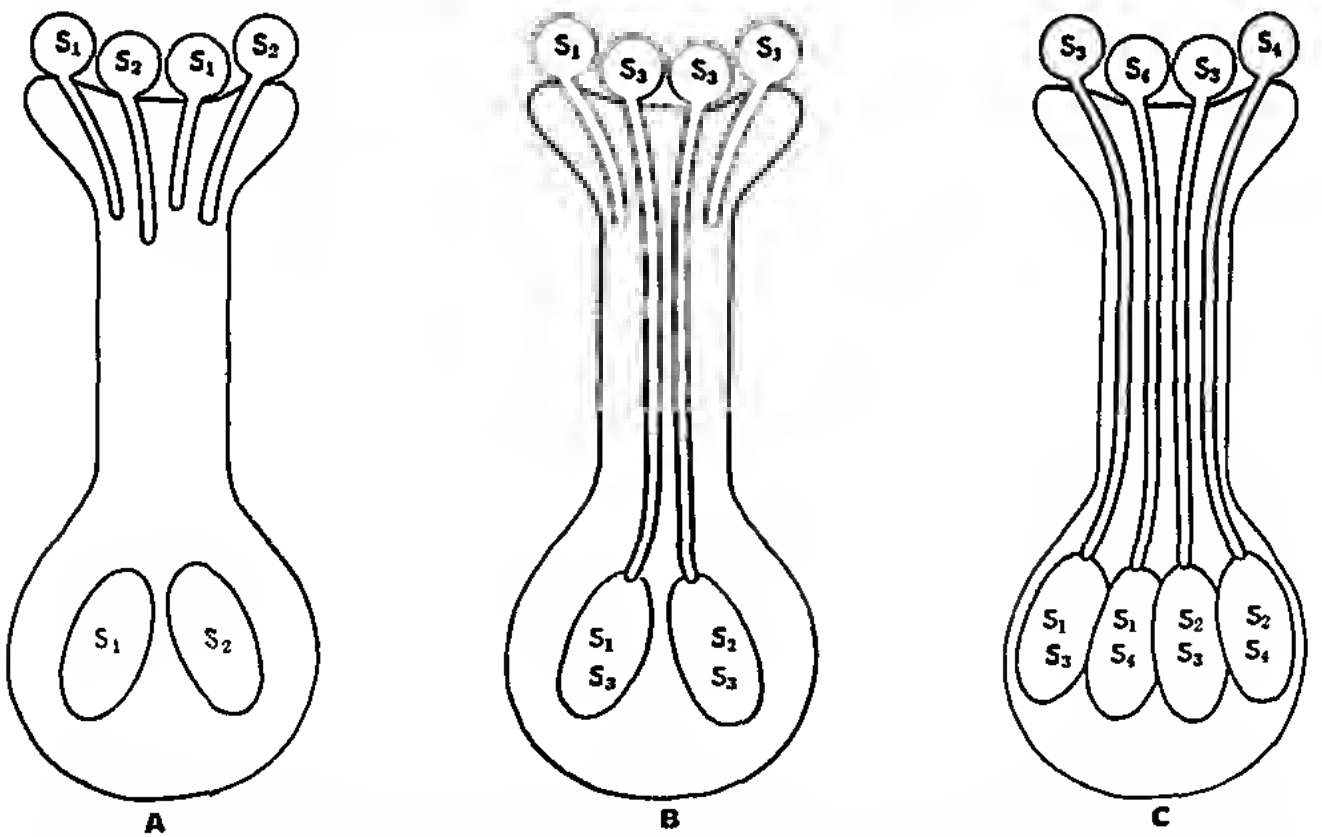


Fig 3 17 Pollen tube growth in compatible and incompatible pollinations A Pollen tubes do not grow in styles carrying similar alleles for incompatibility B Only pollen grains with different incompatibility alleles from those in the style develop normal pollen tubes C All pollen grains carry different incompatibility alleles from those in the styles and develop normal pollen tubes

sterility may be controlled by the action of specific genes or by hereditary mechanisms in the cytoplasm

Genetic Controlled Male Sterility. In some crops, inherent male sterility has been observed that is entirely the result of gene action This type of male sterility has been found in barley, maize, sorghum, wheat, lucerne, sugar beets, and other crops In barley, a simple recessive gene pair (*ms ms*) results in the production of sterile anthers The dominant gene (*Ms*) results in the production of fertile anthers In this crop, genetic male sterility may be used to eliminate the emasculation procedure when making crosses[23] The recessive male-sterile gene is introduced first into a line that is to be used extensively as the female parent in a crossing or backcrossing program of breeding The male-sterile line may then be artificially cross-pollinated without the necessity of its being emasculated The male-sterile line is maintained by pollination from a male-fertile line that is identical in genotype, except that the latter line carries the dominant gene for male fertility

Cytoplasmic Controlled Male Sterility. This type of male sterility is controlled entirely by the action of the cytoplasm Genetic factors are not involved, except as they may modify the action of the cytoplasm Since the cytoplasm is transmitted through the egg only, with the sperms contributing an insignificantly small bit of cytoplasm to the zygote, cytoplasmically inherited male sterility will be transmitted only through the mother parent The action of cytoplasmically inherited male sterility may be modified by the action of pollen-restoring genes The genes are located in the chromosomes and will be contributed both by the male and female parents Cytoplasmic male-sterile plants contain sterile (*S*) cytoplasm Male-fertile plants contain normal (*N*) cytoplasm

Cytoplasmic male sterility has been found in the Italian Red onion[10] In the onion, male fertility is restored by a dominant gene *Ms* Male-sterile onion plants have sterile cytoplasm and the recessive genes for male sterility (*S ms ms*) Male-fertile onions may have sterile cytoplasm and the dominant gene for fertility (*S Ms Ms* or *S Ms ms*), or normal cytoplasm and any combination of the genes for fertility (*N Ms Ms*, *N Ms ms*, or *N ms ms*) Cytoplasmic male sterility has been used in the production of hybrid onions (Fig 3 18)

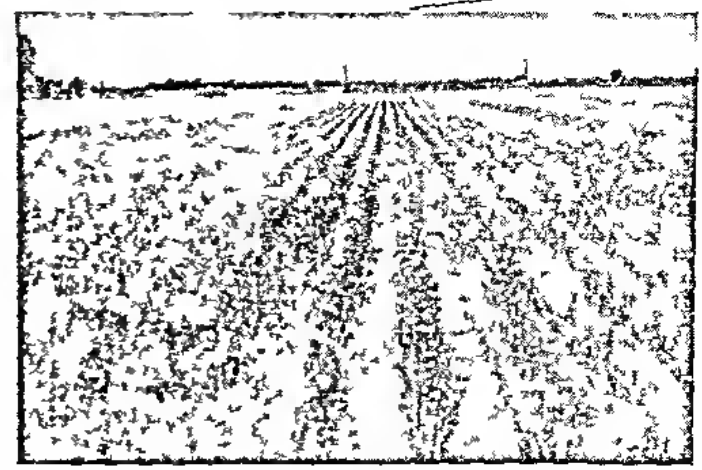


Fig 3 18 Male sterility is used in this commercial onion seed production field in California The light rows are male sterile, i e , they do not produce functional pollen The dark rows produce normal pollen The male sterile flowers are pollinated by pollen carried to them by insects from the normal rows Thus only hybrid seed is produced on the male sterile rows

The original Italian Red 13-53 male-sterile line (*S ms ms*) can be propagated from head sets or bulbils, or by backcrossing to a fertile counterpart that has normal cytoplasm and the recessive genes for male fertility (*N ms ms*) Only male sterile plants will be produced from this cross Hybrid onions are produced by crossing the male sterile line to an unrelated fertile (*N*) inbred line Similarly controlled male sterility has also been found in maize, linseed, sugar beets, sorghum, wheat, bajra, tobacco, and other crops

Utilization of cytoplasmic male sterility in the technique of hybridization will be discussed in the chapters on wheat, maize, sorghum, and millets.

INTERSPECIFIC HYBRIDIZATION

The system of classifying plants into species is based on the natural relationships between groups of plants as determined largely by their morphological and physiological characteristics Although subject to change as knowledge about the relationships of these groups increases, the classification was worked out to a large extent before the science of genetics was developed and without present day information on chromosomes and genes As a result it is difficult to make generalizations regarding the breeding behaviour in interspecific and intergenetic hybridization *The results of interspecific crossing may range from failure to obtain any seed set*

upon crossing to complete fertility in the F_1 plant Some examples of successful interspecies crosses which exhibit different cross fertility relationships are as follows

1 *Crosses between species which are highly cross-fertile* These are crosses between species which have similar chromosome numbers and more or less complete chromosome homology The chromosomes in the F_1 hybrids pair regularly at meiosis, and the F_1 plants are self fertile Examples of species crosses which produce fertile F_1 hybrids that set seed freely are

Avena sativa (cultivated white oats, $2n=42$) × *A byzantina* (cultivated red oats, $2n=42$)

Triticum aestivum (common wheat, $2n=42$) × *T compactum* (club wheat, $2n=42$)

Glycine max (cultivated soybeans, $2n=40$) × *G ussuriensis* (wild soybeans, $2n=40$)

Gossypium hirsutum (American Upland cotton, $2n=52$) × *G barbadense* (American Egyptian cotton, $2n=52$)

Zea mays (Indian corn or maize, $2n=20$) × *Euchlaena mexicana* (teosinte, $2n=20$)

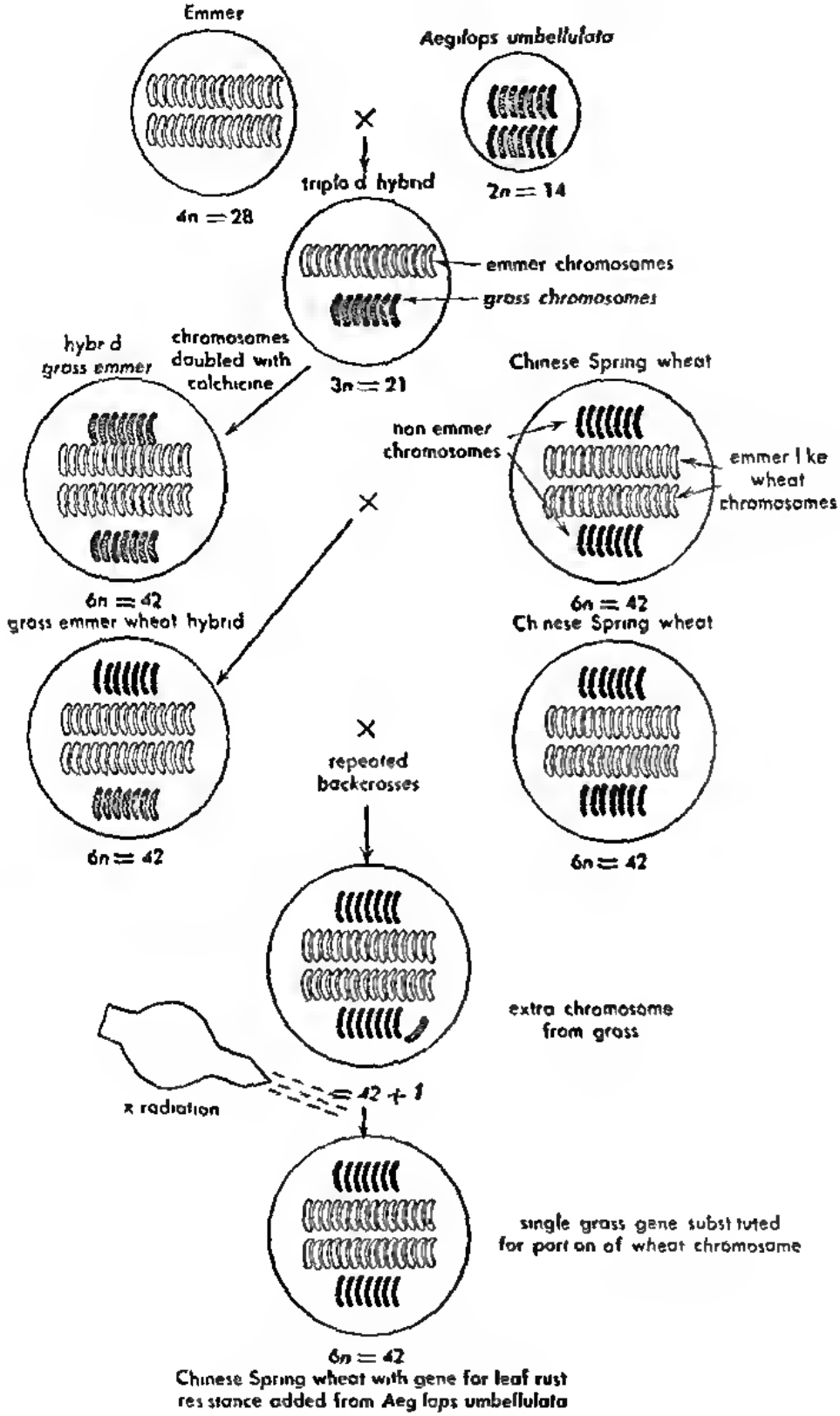
2 *Crosses between species accompanied by doubling of the chromosome complements* Another type of species crossing leads to an increase in chromosome number by the doubling of the chromosomes The amphidiploids of *Brassica*, discussed in the topic on polyploidy, are examples of natural amphidiploids The origin of the tetraploid species of *Brassica* was demonstrated experimentally by combining genomes from two diploid species Where the chromosome content permits the experimental production of amphidiploids, the procedure is to cross the species in question and then double the chromosomes of the F_1 hybrid with colchicine Not all artificially produced amphidiploids will be fertile and set seed Amphidiploids which are fertile and set seed have been produced with species of *Brassica*, *Triticum*, *Gossypium*, *Nicotiana*, and in other genera

3 *Crosses between species with different chromosome numbers* (without doubling of chromosome number in the progeny) Certain interspecific crosses may be made with varying degrees of success, between species which have different chromosome numbers For example, *Triticum durum* ($2n=28$) may be crossed with *T aestivum* ($2n=42$) In *Triticum* the basic chromosome number is 7 *T durum* is a tetraploid species with the genome formula, *AABB*, and *T aestivum* is a hexaploid species with the genome formula, *AABBDD* Thus each parent in a cross between these species would have four genomes, *AABB* (28 chromosomes), in common. The F_1 hybrid plant would have 35 chromosomes (*AABBD*) Occasional gametes would be formed in the F_1 with 21 chromosomes (*ABD*) The chance pairing of two gametes with 21 chromosomes each would give F_2 plants with the full chromosome complement of the hexaploid *aestivum* parent (*AABBDD*) The occurrence of such hexaploid plants would be rare Crosses may sometimes be made successfully between closely related diploid and tetraploid species by first doubling the chromosome number of the diploid, so that it matches the chromosome number of the tetraploid species

F_1 hybrid plants from many interspecific crosses are infertile In crops which may be propagated vegetatively, vigorous F_1 hybrids may be used as the source of new varieties even though they do not set seed This procedure is used in sugarcane which is propagated by stem cuttings, to utilize hybrid vigour from species crosses.[12] It may also be used to utilize hybrid vigour from species crosses in forage crops

GENE SUBSTITUTION FROM ALIEN CHROMOSOMES

Interspecific and intergeneric crosses are frequently attempted by the plant breeder to introduce a desirable character from closely related wild species into a cultivated species In some wide crosses the transfer may be successfully accomplished with relative ease Examples of interspecific crosses which produce fertile hybrids have already been cited In other crosses, where the parent species differs in chromosome number and homology, the crosses are more difficult In crosses between widely differing species the breeder usually wishes to transfer only a single gene for a superior character like disease resistance from the wild to the cultivated species This can be accomplished only by an exchange of a very small segment of a single chromosome from the wild species, which bears the desired gene, with a corresponding segment of a homologous chromosome from the cultivated species In this exchange it is important that deleterious and undesirable genes should not be brought in with the desired gene, otherwise the yield and quality of the culti


Emmer
4n = 28
Aegilops umbellulata
2n = 14
triploid hybrid
3n = 21
emmer chromosomes
grass chromosomes
hybrid grass emmer
chromosomes doubled with colchicine
6n = 42
grass emmer wheat hybrid
Chinese Spring wheat
non emmer chromosomes
emmer like wheat chromosomes
6n = 42
Chinese Spring wheat
6n = 42
6n = 42
repeated backcrosses
extra chromosome from grass
x radiation
= 42 + 1
single grass gene substituted for portion of wheat chromosome
6n = 42
Chinese Spring wheat with gene for leaf rust resistance added from Aegilops umbellulata

3 20A 3 20B 3 20C

Fig 3.20 Parent species used in hybridization shown in Fig 3 19 A Emmer (*Triticum dicoccoides*) B Wild grass (*Aegilops umbellulata*) C Chinese Spring wheat (*Triticum aestivum*)

vated species may be impaired A successful exchange might thus be limited to a segment of the chromosome bearing a single gene An example, in which x-radiation was used to effect such a gene substitution, will be described here [17]

Few varieties of common wheat, *Triticum aestivum*, are highly resistant to leaf rust. Some related wild grasses, however, are practically immune to the disease One of these wild grasses, a native of the Mediterranean area, is *Aegilops umbellulata* Common wheat is a hexaploid species having six genomes each with seven chromosomes ($6n=42$) *Ae umbellulata* has two genomes, each with seven chromosomes ($2n=14$) Differences in chromosome number as well as the genic content of the chromosomes prohibited a direct cross between the species, so a cross was made first between emmer (*T dicoccoides*) and the wild grass, *Ae umbellulata* (Figs 3 19, 3 20) Emmer is a tetraploid species with four genomes of seven chromosomes ($4n=28$) The triploid hybrid ($3n=21$) produced was infertile, but by doubling the chromosome number with colchicine, a fertile amphiploid ($6n=42$) was produced (Fig 3 19) This fertile grass emmer hybrid now possessed 42 chromosomes, the same number as common wheat Of the 42 chromosomes in the hybrid plant, four genomes of seven (the 28 chromosomes derived from emmer) were similar to four genomes of seven, or 28 of the chromosomes in common wheat.

The grass emmer hybrid was next crossed to Chinese Spring, a variety of common wheat The grass emmer wheat hybrid plant contained 42 chromosomes, but was self sterile owing to difficulties in pairing The 14 chromosomes derived from emmer, and the 14 emmer like chromosomes derived from the Chinese Spring variety were related closely enough that they would pair when meiosis occurred in the hybrid plant However, the set of seven chromosomes derived from the wild grass and the set of seven chromosomes derived from the Chinese Spring variety were dissimilar and had no mates with which to pair As a result they behave irregularly at meiosis, and pass at random to the daughter cells Some gametes might receive no grass chromosomes, others might receive as many as seven

The next step was to backcross the grass-emmer wheat hybrid to the Chinese Spring variety By this procedure it was hoped to recover more of the wheat chromosomes In the second backcross generation a hybrid plant with 43 chromosomes

was obtained that looked like Chinese Spring wheat, but which was leaf rust resistant like the grass parent. By further study of this plant and its progeny, it was established that the plant contained the 42 wheat chromosomes and, in addition, one chromosome from *Aegilops umbellulata* bearing the gene for rust resistance (Fig 3 19) It also appeared that certain undesirable genes were carried on the *Aegilops* chromosome, since fertility and vigour of the 43 chromosome plants were reduced

To induce a possible chromosome rearrangement, plants with the 43 chromosomes were x rayed before flowering The pollen subsequently formed was used to pollinate plants of Chinese Spring Among the offspring, one plant was found without the undesirable grass plant features, yet it retained the rust resistance It appeared that in this plant a single gene for rust resistanee was transferred to the middle of a wheat chromosome (Fig 3 19) There is no evidenee that any of the deleterious genes from the grass chromosome were transferred to the wheat.

A wheat variety, named Transfer, has been developed from the rust resistant plant obtained in the eross between *Aegilops umbellulata* and Chinese Spring described above While Transfer was not a desirable variety from an agronomic standpoint, the rust resistance gene obtained from *A umbellulata* has since been transferred from Transfer to varieties of wheat grown commercially in the U S A and Canada

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4

Methods of Breeding Field Crops

The work of the plant breeder is to develop better varieties In this chapter we are concerned with the methods by which new varieties of crop plants originate Before we proceed into a discussion of these methods, let us consider the question, 'What is a variety?"

WHAT IS A VARIETY?

The variety as an agronomic unit is familiar to breeders and cultivators alike The breeder develops and tests new varieties Seed of the new varieties is increased and made available to the cultivator From the available varieties the cultivator chooses those he wishes to grow In spite of this common acceptance of the variety concept, it is exceedingly difficult to describe with accuracy our concept of a variety This requires an understanding of the system by which the plant kingdom is divided into small groups of similar and closely related plants In this scheme *families* of plants are divided into *genera*, which in turn are subdivided into *species*, within the species there may be numerous agricultural varieties The agricultural *variety*, also called *cultivar*, is a group of similar plants which by structural features and performance may be identified from other varieties within the same species

Perhaps this relationship can be clarified by using a common crop plant, rice, as an example. Rice is a member of the grass family The scientific name of the common cultivated rice is *Oryza sativa*, the first word designates the genus, the second word the species All of the rice cultivated in south and southeast Asia is classified within this single species, but not all of the kinds of rice grown are exactly alike They differ in maturity, height, tillering ability, grain characteristics, disease resistance, and in a host of other ways The species *Oryza sativa* is divided into many agricultural varieties or cultivars which are distinguished from each other by heritable traits such as these A classification of rice would thus read as follows

Family, *Gramineae*
Genus, *Oryza*
Species, *sativa*
Agricultural varieties, Prasad Bhog, Dular, PTB 10, Basmati, Taichung Native 1

A superior variety for any area will have a combination of traits that enable it to produce good yields of acceptable quality Genetically, the differences in the identifying characteristics of varieties result from differences in the dominance or recessiveness of specific genes The work of the plant breeder is to find or create groups of plants with combinations of genes that will produce the most favourable growth under a particular set of conditions

Innumerable genetic types are possible within any single crop species These are variously referred to by the plant breeder as *strains experimental strains*, or *lines* Thousands of strains are tested experimentally by the plant breeder each year Once a superior strain is recognized, it may be named, increased and made available commercially as an *agricultural variety* or *cultivar* (also *commercial variety*, or just *variety*, as the term is most commonly used) The distinction of being named and made commercially available serves to set apart the agricultural variety from the experimental strain

How much genetic variability will be found within an agricultural variety? That depends upon the mode of fertilization within the crop and the circumstances under which the variety was developed Most agricultural varieties are pure for those characteristics which identify the variety F example, one variety of have fine g whereas another variety ns A

with a mixture of both fine and coarse grains would be unattractive to the grower, and would generally be considered as mixed or lacking in purity So the breeder strives for uniformity in performance of the plants It is not necessary, however, that a variety be pure for all its characteristics In self fertilized crops, where individual plants tend to be homozygous, the range of purity within a variety will depend upon its origin and genetic stability Some varieties of self pollinated crops are increased from a single genotype (*pure lines*) whereas others are increased from a mixture of genotypes (*mass selections*) The origin of pure lines and mass selections will be discussed in a later topic In cross fertilized crops, where individual plants are heterozygous for many characters, the range of purity within a variety may be quite wide Often it varies from one generation to the next For this reason the "variety" is less of a distinct entity in the cross fertilized crops than in the crops that are self fertilized This contrast in varietal purity should become clearer as the methods of breeding self pollinated and cross-pollinated crops are studied

ACCLIMATIZATION

When a crop plant is introduced into a totally new production area, it may be less adapted than in the climatic area where it was accustomed to being grown In certain cases newly introduced species, which at first were seemingly not well adapted, have after a few seasons established themselves and have become more productive The ability to become inured or adapted to a new climate is referred to as acclimatization To what extent can the acclimatization process change a newly introduced crop, or variety, so that it becomes habituated to its new environment? This will be influenced by (*a*) the mode of pollination, (*b*) the range of genetic variability within the crop, (*c*) the longevity of the crop

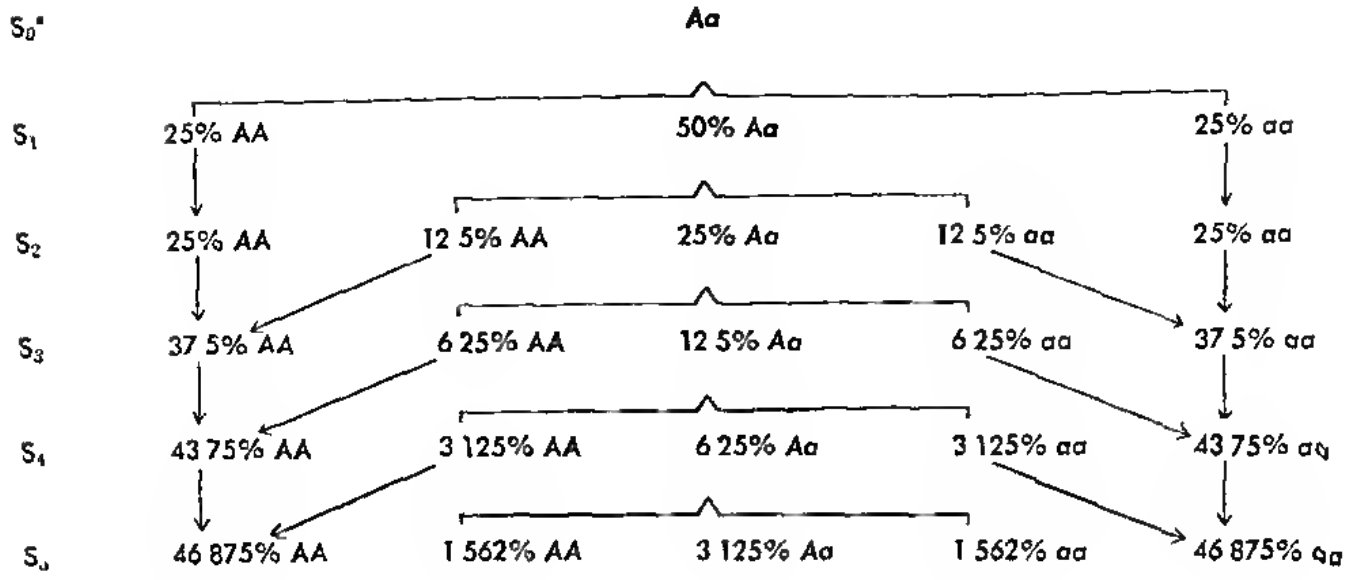
A crop or a variety of a crop becomes acclimated only by an increase of the genotypes within the population that are better suited to the new environment than are the average of the genotypes originally present Acclimatization is natural selection operating in a heterogeneous population of plants It proceeds more rapidly in a cross-pollinated crop than in a self pollinated crop, since gene recombinations will occur with greater frequency owing to the frequent cross pollinations, and some of the recombinations may be more favourably adapted in the new environment In annual crops, gene recombinations occur more frequently than in perennial crops, and thereby increases the possibility that favourable combinations will arise On the other hand, a pure line would change very slightly if at all, and hence would not generally be subject to acclimatization The rate of mutation within the crop is another genetic force which may influence acclimatization Also, gene combinations may react *differently in different environments*

GENETIC SIGNIFICANCE OF *POLLINATION METHOD*

For the breeder to understand the results of selection within a mixed population, it is necessary that he knows something about the genetic nature of the plants with which he is working Plants that are normally self pollinated differ in genetic make up from plants that are normally cross pollinated In a crop that is self pollinated it is the rule that plants will be homozygous This assumption may be made since (*a*) homozygous gene pairs (*AA* or *aa*) will remain homozygous with self pollination, (*b*) heterozygous gene pairs (*Aa*) will segregate producing homozygous and heterozygous genotypes in equal proportions With self pollinations, heterozygosity is reduced by one-half with each successive self fertilization This is illustrated by the diagram on the opposite page

After several successive generations of self pollination, the proportion of heterozygous plants remaining in a population is very small Even though complete homozygosity for all characters is virtually unattainable, at least from a theoretical standpoint, a practical state of homozygosity is normally reached by the breeder after six to eight generations of selfing For qualitative characters in which the dominant may be visibly distinguished from the recessive form, complete homozygosity is desired in order to produce a variety uniform in appearance

A mixed population of a self pollinated crop is in reality a mixture of homozygous genotypes If the individual homozygous genotypes are isolated and increased each produces a pure population. Heterozygous plants may arise in a homozygous population of a self pollinated crop by natural cross pollination or by mutation, but the progenies



* S_0 = original selfed plant S_1 = first selfed generation S_2 = second selfed generation and so on

of these heterozygous plants quickly segregate again into true breeding genotypes

In naturally cross pollinated crops, individual plants are extremely heterozygous as a result of the mixing of the genotypes in each generation by crossing In these species, self-pollination does not normally take place to any significant extent unless pollination is controlled Continuous self pollination, or inbreeding, for several generations in normally cross-pollinated species is generally accompanied by a loss of vigour and productiveness This has been well illustrated in the breeding of hybrid maize in which inbred lines are greatly reduced in size and vigour in comparison with open-pollinated varieties from which they are derived (Fig 3 8) Self fertilization is difficult to attain in some cross pollinated species on account of the presence of incompatibility alleles

In a few crops such as sorghum and cotton there are varying amounts of self and cross pollination In these crops the amount of homozygosity or heterozygosity will vary according to the pollination since there are two opposing forces in action, self pollination, which leads to segregation and homozygosity, and cross pollination, which increases the heterozygosity

METHODS OF BREEDING SELF-POLLINATED CROPS

The principal methods by which new varieties of self pollinated crops originate are (*a*) introduction, (*b*) selection, and (*c*) hybridization The essential features of each of these methods of breedings are related here, and examples are cited to illustrate how specific varieties have originated by each In practice, a breeder may deviate considerably from the methods outlined, although the principles upon which his procedures are based may be unchanged One consideration to be remembered in the breeding of self pollinated crops is that a large number of genetically different plants may be grown side by side in the field with natural reproduction Although varying amounts of natural cross pollination occur in normally self-pollinated crop plants, the amount in most crops is so small that it can be ignored from a breeding standpoint

Introduction. The origins of many of the field crops grown in south and southeast Asia and the records of their early cultivation or introduction into this area are mostly lost in antiquity This includes such commonly cultivated crops as rice, wheat, barley, jute, sorghum, millets, pulses, and sugarcane A few of the important cultivated crops which originated in the Americas were introduced for cultivation into southeast Asia at a comparatively more recent date Among these crops are maize, tobacco, potatoes, and some species of

Early introductions were made for t
by traders and merchants and diver
strains were imported by them B
trial and error, the varieties with

adaptation to the various crop producing regions gradually became known, and their use was extended in those regions Unadapted varieties were eventually dropped from production

The initial step in a breeding programme with any crop is to accumulate a collection of diverse genotypes which may be used as source material for desirable genes The germ plasm collections may include both local and exotic strains of the crop species and closely related species While the breeder may collect local strains from the cultivator or from other breeders in nearby states, he must usually rely on central governmental agencies to supply him with exotic varieties since their collection and maintenance requires special skills and facilities which are too expensive to duplicate in every breeding programme

One of the first planned, large scale programmes for the systematic introduction of new crops and new crop varieties was initiated by the United States Department of Agriculture In 1898 an Office of Foreign Seed and Plant Introduction[14] was established and plant scientists have since been sent all over the world to find and collect plant and seed stocks of crops both old and new, which might be useful to the American plant breeders in the development of improved crop varieties While many useful species and varieties were introduced as a result of this programme, perhaps none became more extensively cultivated or economically more important in the U S A than the soybean, a plant long cultivated in China, Japan, and other countries in Asia Over 10 000 strains of this single crop alone, representing 2 500 distinct types were collected from the Asiatic area,[16] 3,000 strains as the result of a single organized expedition Large '*World Collections*' of introduced and local strains of wheat, barley, oats, rice, sorghum maize, and other field and horticultural crops have been assembled and are being maintained by the Plant Introduction division of the United States Department of Agriculture These collections are available to American plant breeders and plant breeders in other countries, and from them the breeder can augment the resources of germ plasm already available to him These collections become increasingly valuable to the breeder as native strains disappear from cultivation as the result of the distribution of new and improved varieties

Fig 4 1 Cuba 342 2 2 f # # a maize inbred line used in India Introductions from Mexico Central America and the southern U S Corn Belt are used extensively in the breeding of hybrid maize in India

In addition to the collections of the United States Department of Agriculture, large collections of wheat, oats cotton and other crops have been made and are being maintained in Russia and many other countries Over 10,000 strains and varieties of rice are being maintained by the International Rice Research Institute, Los Banos the Philippines and over 3,000 strains at the Central Rice Research Institute, Cuttack, India (Fig 4 1) Sugarcane collections are being maintained at the sugarcane breeding stations at Canal Point, Florida U S A, and Coimbatore, India and in other countries Many strains of maize have been introduced into India from Mexico, Colombia, and other South American countries by the Indian Agricultural Research Institute, New Delhi, in cooperation with other organizations including the Rockfeller Foundation in India and Mexico

In India, the introduction, maintenance and evaluation of plant materials are vested in a Division of Plant Introduction with headquarters

at the Indian Agricultural Research Institute, New Delhi Over 25,000 indigenous and exotic plant or seed collections have been made and explorations are being conducted in various locations in India and surrounding areas Plant and seed materials maintained by the division are supplied to plant breeders in India and materials are exchanged with other countries The import of living plant materials into India must be accompanied by a certificate of health to prevent introduction of new pests or diseases, otherwise the materials will be destroyed at the port of entry by plant protection and quarantine workers New introductions, upon being received, are given an identifying number and information s recorded on origin, adaptation, and characteristics insofar as available Three groups of materials are maintained, each group being identified by letters prefixed to the numbers These groups and the prefixes are (*a*) E C, exotic collection, (*b*) I C, indigenous collection, and (*c*) I W, indigenous wild It is therefore possible from the prefix to identify whether the plant is a local or introduced strain and if a local strain, whether wild or cultivated

After seeds or plant stocks of a crop are introduced they must be catalogued, made available to breeders interested in testing them, and maintained in a viable condition so that they may be used again at some future date Maintaining viable seed or plant stocks is particularly important since the world collections are the best reservoirs of plant germ plasm available to breeders in the future To evaluate these large collections of germ plasm for breeding stocks it is necessary to grow them in various agroclimatic regions in order to determine where particular strains may be adapted For example, in India, regional substations are being developed by the Division of Plant Introduction representing regions in which crops adapted to different climatic conditions may be grown and evaluated For example, non hardy tropical or semi tropical types may not survive the rigours of a northerly climate, or photo-sensitive varieties may not flower if grown in a climatic area with unsuitable day lengths The location of these stations and the climatic zone represented are as follows (*a*) temperate zone, Simla, (*b*) arid zone, Jodhpur, Rajasthan, (*c*) tropical zone, Kanyakumari Madras, and (*d*) mixed climatic zone, Amarvata, Maharashtra With some crops, in which organized breeding programmes are functioning with adequate facilities for testing, such as in sugarcane, rice, maize, sorghum and wheat, collections are maintained and new introductions are evaluated by these organizations instead of the Division of Plant Introduction at New Delhi Disease and insect resistance can only be evaluated by growing the strains under conditions where they are exposed to the disease or insect under study, either under natural field conditions, or by using techniques for artificial inoculation or infestation Recently the entire U S D A world collection of sorghums, containing several thousand entries, was grown at several locations in India in order to evaluate the breeding potential of the strains in that collection under Indian conditions With many crops, quarantine glasshouses or detention nurseries have been established where new introductions are fumigated and grown under quarantine in an isolated area before distribution to areas of commercial production This precaution is taken in order to prevent the introduction of new plant diseases and insects into production areas

Commercial varieties of field crops may originate from introductions by (*a*) growing the variety as introduced *en masse*, (*b*) selection of desirable strains from the introduced stock, or (*c*) using the introduced variety as a parent in a cross Examples of commercial varieties of self pollinated crops that have been developed by each method follow

Example of (*a*) The wheat variety, Ridley, introduced into India from Australia, was found to be resistant to black and brown rust; moderately resistant to loose smut, and to possess good yield and grain quality Ridley is recommended and grown in several areas in India

Example of (*b*) A collection of mung (*Phaseolus aureus*) was obtained from China The original variety was poor in yield and had dull seed colour From this collection twenty plants were selected of which four were resistant to chlorosis One of the resistant plants had larger seed size and brighter seed colour Seed from this plant was increased and released as a new variety in Punjab, Shi[illegible] Mung No 1

Example of (*c*) Four rust resist[illegible] of linseed were sent to India fr[illegible] These strains were crossed with [illegible] of linseed that were rust st[illegible]

crosses 128 rust resistant strains were selected One of these later named N P R R 9 was increased as a new variety The rust resistant collections from Australia had originated in the U S A and had been selected for linseed wilt resistance by Dr Bolley The new variety, N P R R 9, was also resistant to wilt

As improved varieties adapted to specific local environments are developed fewer and fewer of the introduced varieties of standard crops will be superior to the local varieties already in use However, the introduced varieties may possess genes for disease or insect resistance, stiff straw, frost hardiness, or other desirable features which can be transferred to adapted varieties by hybridization

It has been suggested by Vavilov, a Russian scientist, that the centre of genetic diversity of a species will be in the general region of its origin [26] From extensive studies, he designated eight principal regions of origin for cultivated plants, later this number was increased to twelve [3] Seven of the regions of origin are in Eurasia and Africa, four are in South and Central America and one is in the United States In the past the regions of origin have been the principal areas where new sources of germ plasm might be found The world collections of the principal cultivated crops have been built up, to a large extent, from wild and cultivated varieties found in these areas, but the collections are far from complete With advancement in culture and the cultivation of improved varieties over the entire world many of these centres of diversity are threatened with extinction In the future it may not be possible to go back to these "primitive" areas to find new genes It is important, therefore, that a great array of these diverse varieties be collected before they are lost Southern Asia is rich in local or 'desi' varieties that may have genes useful for present day or future plant breeders With the acceleration in plant improvement programmes in this area, many of the old varieties will be lost within the next decade or two It is important to the future plant breeder that these local varieties be collected now before they are lost forever These collections of plant and seed materials should then be preserved indefinitely as sources of germ plasm for future plant breeders Special attention needs to be given to seed storage facilities for germ plasm collections, especially in the countries of south and southeast Asia where the viability of seeds deteriorate rapidly with the prevailing high temperatures and high humidity By storing seed in a refrigerated room with low humidity, the viability of seeds of most species may be maintained many years whereas the viability would be lost quickly if stored under normal conditions

Selection. Selection is one of the oldest breeding procedures and is the basis of all crop improvement It has been practiced since the earliest time that man began to cultivate crops The present status of our cultivated crops is largely the cumulative result of all the selection that has been practiced through many centuries Essentially, selection is a process, either natural or artificial *by which* individual plants or groups of plants are sorted out from mixed populations The efficacy of selection is dependent upon the presence of genetic variability Two methods of selection are practiced in breeding new varieties of self pollinated crops These are *(a) mass selection* and *(b) pure line selection.*

A MASS SELECTION If a group of similarly appearing plants is selected and harvested, and the seed is composited, the selection procedure is known as mass selection A mass selection of a self pollinated crop will be a composite of more or less similar and supposedly true breeding genotypes A variety developed by mass selection will generally be more or less pure for those physical features which may be easily seen and used as the basis for purification such as presence or absence of awns, colour markings, or maturity But its component lines may differ in quantitative characters, such as yield size, or quality since small differences in the quantitative characters cannot be visibly distinguished

In mass selection, *plants are chosen on the basis of the phenotype and the harvested seed is composited without progeny testing* The object is to improve the general level of the population by selecting and bulking the superior genotypes already present A *general procedure* for developing a variety by mass selection is outlined

First year Select a few to several hundred plants with similar phenotype Harvest and composite seed

Second year Grow in preliminary yield test, comparing with standard varieties as check If mass selection is used to purify an old mixed variety the variety from which it was selected should be

included as a check Observe comparative height, maturity, lodging, disease resistance, yield, quality or other appropriate characters

Third to sixth years Continue in yield tests to determine performance and adaptation in comparison with standard varieties as checks

Seventh year Start seed increase for distribution

When used as a method of breeding self pollinated crops, mass selection has two weaknesses 1 It is not possible to know whether the plants being grouped are homozygous or heterozygous for specific dominant characters Since the heterozygous plants will segregate in the following generation, phenotypic selection may need to be repeated

2 The environment in which a plant grows affects its development and appearance With mass selection it is not possible to know whether the selected phenotype is superior in appearance owing to hereditary characters or to environment

Mass selection is often used to purify mixed varieties When mass selection is used to purify a mixed variety, testing may be terminated and seed increase started any time after it has been verified that the new strain does not differ in adaptation and performance from the mixed variety and that it is superior to the mixed variety in uniformity

B PURE LINE SELECTION A progeny descendent solely by self pollination from a single homozygous plant is known as a pure line A pure line variety is developed by increasing the self fertilized progeny from a single, true breeding plant A variety developed by pure line selection is more uniform than a variety developed by mass selection since all the plants in the pure line variety will be exactly alike This is assuming, of course, that the plant originally selected is homozygous for all gene pairs, an assumption which plant breeders often make, but a condition which is seldom, if ever, completely realized Shining Mung No 1 is an example of how a pure line selection may be made from a population of mixed genotypes In this example the original population was an introduced or exotic collection of seed but many of the old local or "desi" varieties are comprised of mixtures of genotypes Many varieties are developed by pure line selection from mixed populations in the early stages of a breeding programme with a self pollinated crop N P 4 and N P 52 wheats were selections made in India from indigenous varieties N P 11 and N P 12 varieties of linseed likewise were pure line selections from indigenous varieties Many others will be cited in later chapters on the breeding of wheat, rice, jute, linseed, and other self pollinated crops

Pure line selections are also made from hybrid progenies The N P R.R.9 variety of linseed already cited is an example How hybrid populations are produced by crossing varieties and the selection procedures used to isolate new varieties will be described later in this chapter

A *general procedure* for making pure line selections is outlined Various modifications of this general procedure may be followed in actual practice

First year Select 200 to 1,000 plants from a genetically mixed population of an old variety

Second year Grow progeny of each plant in an individual row Harvest superior progenies and composite the seed from plants within each row Each progeny then becomes an experimental strain

Third year Grow strains in replicated observation plots Harvest only superior strains Strains may be grown in preliminary yield tests, if seed supply permits

Fourth to seventh year Continue in yield tests

Eighth year Choose best strain for distribution and start preliminary increase of seed

Pure line selection may be practiced by cultivators who may observe off type plants in their fields Many useful varieties have been produced in this way The plant is generally the basis for pure line selection but in thickly planted crops where individual plants cannot be separated, single heads from different plants may be selected Pure line selection is practiced within segregating populations after artificial hybridization of two varieties The progeny test is essential in pure line selection in order to evaluate accurately the breeding behaviour of the selected plant

New genotypes are not created by pure line selection Improvement by this method of selection is limited to the isolation of the best genotype already present in the mixed population Once the superiority of a selected strain has been proved by thorough testing procedures, it may be increased, named, and distributed as a new agricultural variety

How long does a pure line variety remain pure? That depends upon the particular cr its genetic

stability, the amount of natural cross-pollination and the care with which it is produced Pure lines may become impure as a result of (*a*) mixtures of seed from other varieties, (*b*) natural crossing with other varieties, and (*c*) mutations

Seed mixtures may occur if proper care is not taken during drying, threshing and storage Rogues or off type plants starting from seeds dropped from another variety previously grown in the same land may also be a source of seed mixtures Natural crossing may occur if two varieties are planted in adjacent fields or in adjacent plots in the breeding nursery before the variety is distributed Natural crossing may occur also between a variety and plants occurring as mixtures in the variety The mutation rate and genetic stability of varieties differ Some varieties remain relatively pure over a period of many years while other varieties are less stable genetically, from them off-type mutant plants may be selected frequently

For many years emphasis was placed on the development of pure line varieties that would be extremely uniform in appearance and performance In recent years the feeling has been growing that such extreme uniformity is unnecessary Sometimes it may be undesirable. This change in viewpoint is based on the supposition that a variety with more genetic variability would (*a*) be productive in a greater variety of environmental conditions and thus more widely adapted, (*b*) produce more stable yields when seasonal conditions vary, and (*c*) offer broader protection against disease [15]

Objections to mixed or multiline varieties are based on their being (*a*) less attractive than a uniform variety, (*b*) more difficult to identify in a seed certification programme, and (*c*) generally lower yielding than the best line within the mixture

C THE PURE LINE THEORY The theory of the pure line was established by a Danish botanist, Johannsen, in 1903 Johannsen conducted selection experiments with a mixed seed lot of the Princess bean He selected from this random lot large and small seeds These were planted and the seeds were harvested from each of the growing plants The seeds harvested from each plant varied in size, but the average weight of the progeny from the large seed was larger than the average weight of the progeny from the small seed This indicated that the selection had been effective in separating

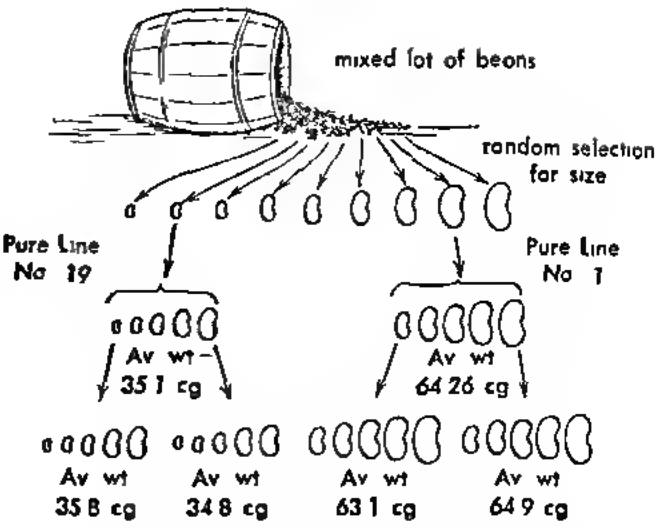


Fig 4 2 Pure line selection in beans From a mixed lot of the Princess bean a pure line (Pure Line No 1) was isolated that produced beans averaging 64 26 centigrams in weight Another pure line (Pure Line No 19) produced beans averaging 35 1 centigrams in weight The average seed weights of progenies of beans selected from Pure Line No 1 were similar to those of the parent line Likewise progenies of seeds selected from Pure Line No 19 were similar to their parent line in average seed weight This experiment demonstrated that a mixed population of a self pollinated crop may be separated into pure lines inherently different but that further selection within a pure line is ineffective in changing the genotype of the line

bean seeds that possessed different genes for seed size Since beans are self fertilized, the seeds were pure from the start The original selection was from a mixture of pure lines and was therefore successful in separating beans with different genotypes for size

To test the efficacy of additional selection, Johannsen established nineteen pure lines by selection of individual beans from the mixed lot (Fig 4 2) Within each of these pure lines he again selected a large and a small seed The progenies of the large and the small seeds *from a single pure line* varied in the weight of the individual seed again, but the average weight of the progeny from the large seed was quite similar to the average weight of the progeny from the small seed within the same pure line These results indicated that selection within a population of mixed genetic types, such as the original mixed lot of beans, may be effective in isolating lines that are inherently different But once the pure line has been isolated, further selection within the line is in

effective In the original mixed lot of beans, variations in seed size were both hereditary and environmental Within the pure lines, variations in seed size were due to the environment only

Hybridization. In the hybridization method of breeding self fertilized crops two varieties are crossed, and plants in which are combined the desirable features of the parents are selected from the segregating progenies for increase and testing With hybridization the best characteristics of the parent varieties may be combined into a single, true breeding strain

In a cross between Pusa 4 and Australian Federation varieties of wheat, a strain was selected, N P 165, which combined genes for good yield and quality from Pusa 4 with loose smut resistance genes from Federation In a later cross between N P 165 and Kenya E220, several strains were selected and later released as varieties, which combined genes for high yield, quality and smut resistance from N P 165 with genes for high resistance to black rust and to brown rust from Kenya E220

In addition to combining visible traits of the parent varieties by hybridization, it is also possible to select plants from the progeny of a cross that will be superior to the parents in those features of a quantitative nature, such as yield, straw stiffness, or quality, in which inheritance is determined by multiple genes These superior combinations, known as *transgressive segregates*, were discussed in the last chapter Many important improvements in plant breeding by hybridization come about by slowly accumulating desirable genes for quantitative characters from diverse parental types While the results may not always be as spectacular as when a single character, such as rust resistance, controlled by a single major gene is added to a variety, the progress in the long run may be just as important

In the hybridization method of breeding self-pollinated crops, the parent varieties are artificially cross pollinated Artificial cross-pollination is relatively easy with grains which have large floral parts It is more tedious in crops like lentils and many forage grasses which have similar flowers The technique of crossing consists of removing the anthers before any pollen is shed, collecting viable pollen from the male parent variety, and transferring it to the stigma of the emasculated plant [12 13 20] The exact procedures for emasculation and collecting pollen vary with the crop, and a thorough knowledge of the flowering habits of the crop with which one is working is necessary Selfing and crossing techniques will be discussed in the following chapter on "Techniques in Breeding Field Crops" and in the chapters dealing with specific crops In some self pollinated crops, barley for example, the emasculation procedure may be eliminated by the use of male sterile plants which have sterile anthers and do not produce pollen [25] A recessive male-sterile gene is first introduced into the female parent variety by backcrossing Emasculation is then unnecessary This procedure is practical where a variety is to be used in a series of crosses or backcrosses

If the parent varieties in a cross are pure lines, the plants within the variety will be homozygous and identical The F_1 plants, although highly heterozygous will have similar genotypes and will look exactly alike Genetic segregation will begin with the F_2 generation, and heterozygosity will be reduced by one half with each succeeding selfed generation The number of F_1 plants needed will depend upon the crop and the size of the F_2 progeny that one desires to grow Usually a large F_2 population, from 1,000 to 10,000 plants, depending upon the similarity of the parent varieties and the number of characters from each parent that the breeder desires to combine in the progeny, will be needed to give a wide range of genetic segregation

A SELECTION PROCEDURES AFTER HYBRIDIZATION

Two selection procedures are commonly used after hybridization to sort the desirable genotypes from the segregating progeny (*a*) *pedigree selection*, in which plants with the desired combination of characters are selected in the F_2 generation, and the progenies of each selected plant reselected in succeeding generations until genetic purity is reached, (*b*) *bulk population* method, in which selection is delayed until a later generation, usually the F_5 or F_6 after hybridization, at which time segregation will virtually have ceased

A typical procedure by which each of these methods of selection might be carried out is given with an example of a theoretical cross between a widely adapted variety of wheat, which we will call variety A, and a variety assumed to be resistant to stem rust which we will call variety B We may assume that the purpose of such a cross would be to combine the short, early plant type, disease

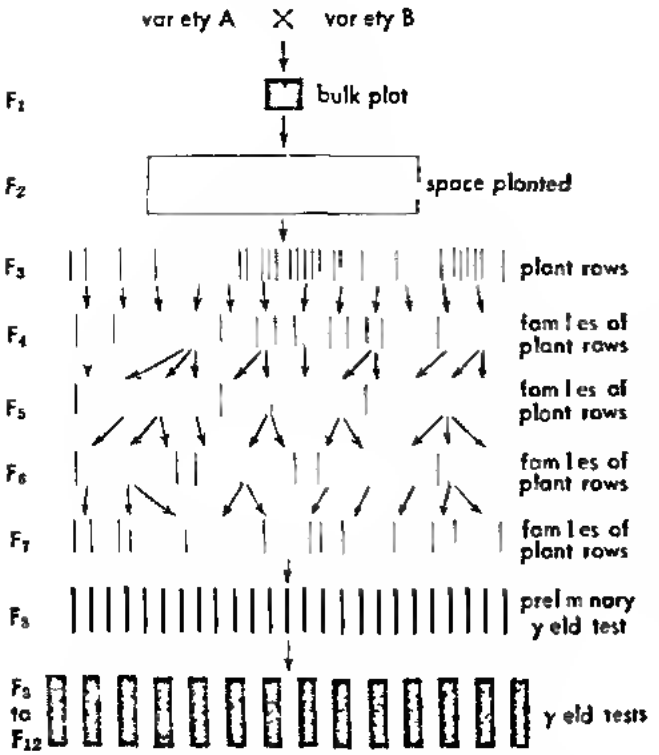


Fig 4 3 Pedigree method of selection From selected F_2 plants progenies of 25 to 30 plants are grown in plant rows in the F_3 Superior plants from the best rows are selected and planted in families of plant rows in F_4 Selection is repeated in F_4 F_5 and F_6 with selection being made of best plants in best rows of best families By F_7 families should be relatively uniform Preliminary yield tests are planted in F_8 and yield tests are continued through the F_{12} Various modifications of this procedure may be made For example after plants are selected in F_3 and F_4 remaining plants in row may be bulked and preliminary yield tests started

resistance, and high yield of variety A with the stem rust resistance of variety B

Example of pedigree method of selection (Fig 4 3)

First year Cross A × stem rust resistant variety B

Second year Grow 10 to 25 F_1 plants

Third year Grow 2 000 to 6 000 F_2 plants The size of the population will vary with the crop, the objectives of the cross, and the facilities available When planting space seeds 3 to 6 inches apart in the row so that individual plants can be examined Inoculate adjacent rows of a rust susceptible spreader variety with stem rust Select several bundred short, early, vigorous plants which look like variety A and which are stem rust resistant

Fourth year Grow F_3 progeny rows from 300 to 500 selected F_2 plants Space seeds in row so that individual plants may be studied Families pure for rust resistance may be reselected for plant type, or resistant plants may be selected from short, early maturing families segregating for rust resistance Normally 50 to 100 families may be retained at the end of the fourth year

Fifth to eighth years Reselect superior families in F_4 to F_7 until each is uniform Only the best appearing and most uniform rust resistant lines should be reselected and carried forward to the next generation The total number of lines carried at the end of this period may be reduced to not more than 25 to 50

Ninth year Grow preliminary yield test

Tenth to thirteenth years Lines remaining are tested for yield in comparison with standard commercial varieties Only the highest yielding lines are retained in the yield tests each year During the testing period, observations are made on height straw stiffness maturity, disease resistance, and quality Superior lines may be grown in regional tests to learn the range of adaptation By the end of the five years of yield testing, not more than two to five superior lines will generally remain If superior to the commercial check varieties one line may be chosen for increase and distribution

Fourteenth and fifteenth years Increase seed and distribute new variety

It will be noted that 14 to 15 years are required to develop a new variety by hybridization with one generation only of the crop grown each year The number of years may be reduced if more than one generation of the crop can be grown per year In tropical and subtropical areas, such as south and southeast Asia it is often possible with many crops to grow two or three generations per year so that the total number of years may be much less than that described here

The pedigree method of breeding can be used advantageously if the characters to be combined in the cross are such that they can be seen easily and used as the basis for selection during the early generations Various modifications of this procedure may be employed For example yield tests may be introduced in the F_4 and F_5 generation, and high yielding lines may be purified in later generations The pedigree method of selection requires much work and careful record taking during the early segregating generations, but it has the advantage that only the progenies of superior plants in which genes for the desirable characters

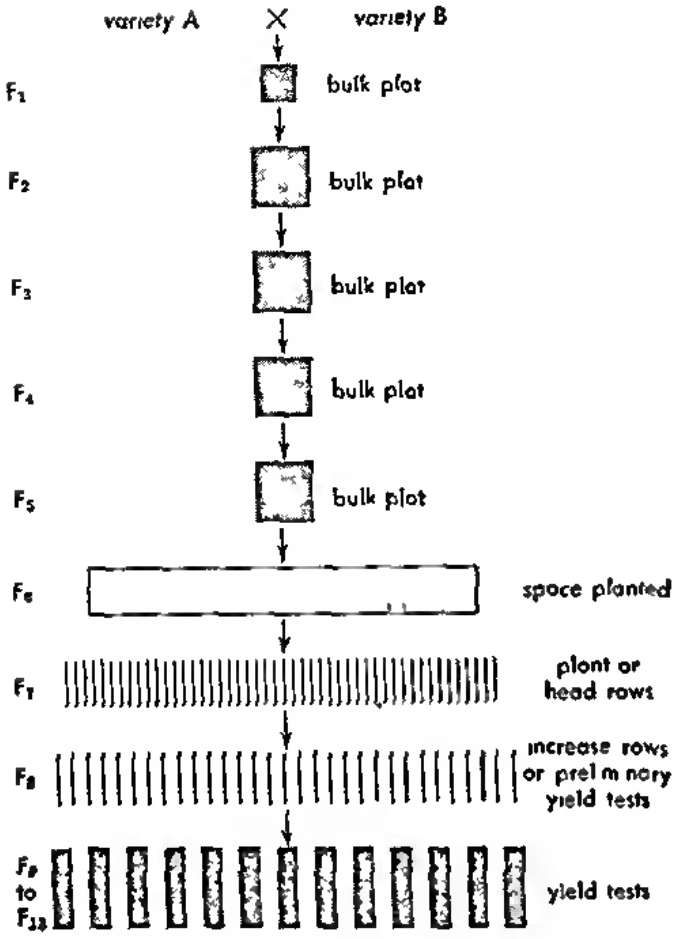


Fig 4 4 Bulk population method of selection The progeny of the cross is grown in a bulk planting through the F_5 generation In F_6 the progeny is space planted Plant or head selections are made and grown in plant or head rows in F_7 Superior rows are selected and grown in increase rows or preliminary yield test in F_8 Superior strains are grown in yield tests in F_9 through F_{12} Various modifications of this procedure may be made For example, selection may start as early as F_3 or F_4 with lines having a superior yield being purified in later generations, or bulk plots may be replicated and harvested for yield and entire crosses discarded on the basis of the yield of the bulk plots

are already combined need to be carried forward to the next generation This method may also allow the plant breeder to obtain genetic information not possible with other systems The pedigree method of breeding is well suited to crops where individual plants may be observed and harvested separately, as in tobacco, cotton, or groundnuts

Example of the bulk population method of selection (Fig 4 4)

First year Cross variety A×stem rust resistant variety B

Second year Grow 10 to 25 F_1 plants

Third year Grow F_2 generation Harvest and bulk seed from all plants

Fourth to sixth years Grow 1/20 to 1/40-acre plots from bulk seed harvested the preceding year

Seventh year Space plant Induce a heavy stem rust epidemic during the F_6 generation and select 1,000 to 5,000 rust-resistant plants, or harvest heads from a similar number of plants if individual plants cannot be identified from each other

Eighth year Grow progenies of selected plants (or heads) in separate rows Harvest 100 to 300 rows which combine short, early, A-type plants and stem rust resistance Desirable rows still segregating may be reselected to establish true-breeding strains

Ninth year Superior lines are grown in single or paired 10-foot rows for increase and additional observation Preliminary yield tests may be conducted if sufficient seed is available

Tenth to fourteenth years Yield tests continued as in pedigree method

Fifteenth year Increase for distribution

The bulk population method of breeding is simple, convenient, and inexpensive Less work is required during the early segregating generations But it is then necessary to grow several thousands of selected plants in order to have a reasonable chance of finding desirable segregates from the bulk populations Subjecting the bulk populations to disease epidemics, winter killing, drought, or other adversities during the segregating generations will foster natural selection in the bulks for these features Lines selected from the bulk that appear to be segregating may need to be reselected to establish true-breeding strains The bulk population method is suited to thickly spaced crops, like small cereals, that are difficult to grow in spaced planting

It should be apparent that the most difficult part of the hybridization method of breeding is to recognize and isolate the desirable plants from the segregating populations after the cross has been made This requires careful observation, exhaustive testing of all selected plants and their progenies, subjection of the selected lines to as many adversities, such as disease, drought, or cold, as possible; detailed and accurate note-taking and record-keeping, and finally on the basis of all available

information, skill of the breeder in identifying with some degree of accuracy the lines that may be potentially desirable This skill is usually enhanced by long experience Only superior lines should be propagated for success in any hybridization programme *Also, for an efficient hybridization programme of breeding parent varieties need to be carefully selected for the traits that they possess so that the desired characteristics may be combined in the progeny of the cross*

Consideration needs to be given to the number of plants selected at each generation This may vary considerably according to the characters with which the breeder is working In the theoretical cross described here rust resistance was the only parental trait desired from the second variety Normally, rust resistance is inherited in a simple manner In such a cross, primary selection would be made for rust resistance because the rust reaction of the plants in the F_2 or in later generations, may be easily identified, if the environment is such that the rust disease is present In this particular cross, the objective is to obtain a recombination of the parental types Frequently, in a cross made to improve a quantitative character, the objective is to obtain transgressive segregates that are superior to the parent varieties Since the expression of quantitative characters is often influenced by the environment, it may be difficult to identify accurately the superior F_2 phenotypes In such a case it may be necessary to harvest a larger number of F_2 plants and grow their F_3 progenies The breeder then has a group of twenty five to fifty plants in each F_3 progeny upon which to observe the characteristics of the progeny

If only one quantitative character is being emphasized in a cross, it should be possible to select transgressive segregates superior to either parent If two or more quantitative characters are being improved, some compromise may be necessary, since one would seldom find transgressive segregation occurring simultaneously for two or more characters This brings us back again to the question of selecting the parents The breeder should have clear and specific objectives in mind when he selects the parent varieties *The parents should clearly be superior in these characteristics The superior characteristics of each of the parent varieties should complement each other*, so that progeny plants will not be lacking in some important agronomic characteristics Otherwise, the variety would be useless to the cultivator, even though the objective of the cross was reached

B MULTIPLE CROSSING A complex system in which eight to sixteen varieties are systematically crossed has been used in the production of new varieties of some self-pollinated crops, particularly barley [10 17] These multiple crosses are produced by crossing pairs of parents, and then crossing pairs of F_1's until all parents enter into a common progeny according to the scheme outlined below

$$\begin{array}{ccccc} A\times B & & C\times D & & E\times F & & G\times H \\ AB & \times & CD & & EF & \times & GH \\ & ABCD & & \times & & EFGH & \\ & & & ABCDEFGH & & & \end{array}$$

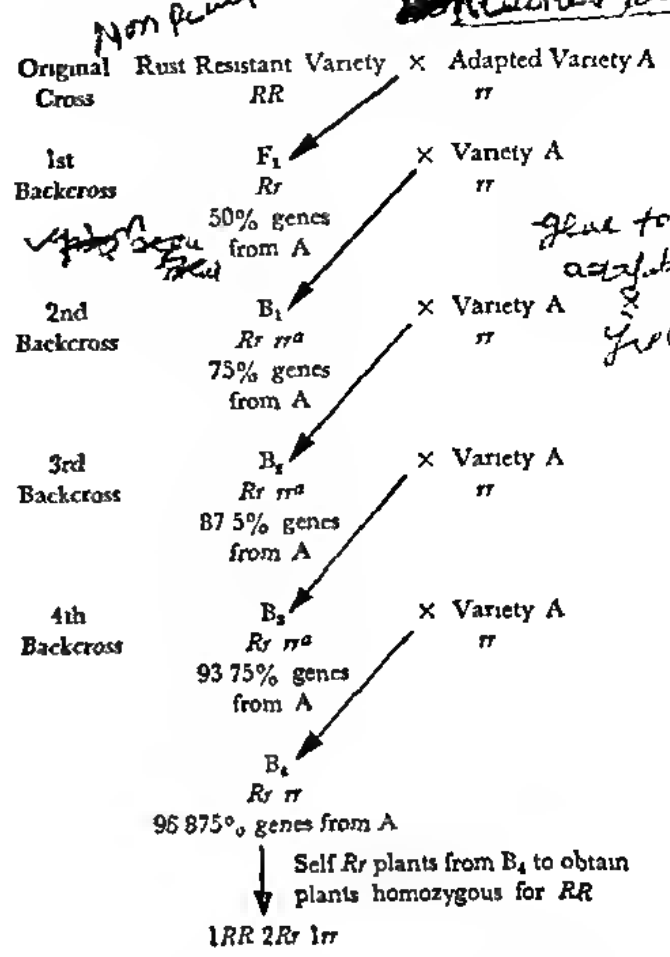
This system of crossing has the advantage of bringing together quickly combinations of genes from several parents Many possibilities of combinations exist since every seed produced after the initial cross is essentially a new hybrid Exceedingly large numbers of hybrid seeds must be obtained in the second and later crosses if the maximum number of possible genotypes is to be represented in the progenies A disadvantage of this system is that many undesirable combinations may be brought together since such a large number of parent varieties is involved The possibility of obtaining desirable combinations would be enhanced by selection within each progeny before the next cross is made, but this procedure will require a longer time to reach the final cross

C THE BACKCROSS The backcross is a form of recurrent hybridization by which a superior characteristic may be added to an otherwise desirable variety [1 2 11] The plan of the backcross is relatively simple Two parent varieties are selected and crossed One parent is an adapted productive variety which lacks some superior characteristic that is found in the second variety Beginning in the F_1, the hybrid material is successively backcrossed several times to the adapted parent variety After each backcross, selection is made for the superior character from the second variety Only hybrid plants possessing the superior character are used in the backcrosses The adapted parent, to which the superior character is being added enters into each backcross and is called the *recurrent* parent The donor parent for the superior

character does not enter into the backcrosses and is called the *nonrecurrent* parent

The purpose of the backcross is to recover the genotype of the recurrent parent, except for the addition of a gene (or genes) for the superior character which is being contributed from the nonrecurrent parent The backcross is a form of inbreeding and the features of the recurrent parent are automatically recovered after successive backcrosses The only selection practiced is for the one superior trait contributed by the nonrecurrent parent The number of backcrosses may vary from one to eight, depending upon how completely the breeder wishes to recover the genes from the recurrent parent The backcross procedure is most easily carried out if the superior character being added is simply inherited dominant, and easily recognized in the hybrid plants

The backcross method may be demonstrated by the hypothetical cross already considered in which genes for stem rust resistant (*RR*) are to be added to a widely adapted variety of wheat, which we will again call variety A This is a suitable example for illustrating the backcross procedure because in it we desire to add a single gene for rust resistance to a widely adapted variety The details of the backcross procedure may be understood more easily by studying the diagram on this page



[a] Only *Rr* (resistant) plants backcrossed to A *Rr* (resistant plants may be identified from *rr* (susceptible) plants by inoculating each hybrid plant with stem rust The inoculations may be made in the seedling stage and the genotype established before the next backcross is made

In this cross variety A is used as the recurrent parent, and contains the genes for adaptation and yield that the breeder wishes to recover in the new variety With each successive backcross, the progeny becomes more like the A variety as additional genes for adaptation from variety A become fixed in the progeny The F_1 from the original cross will be heterozygous for rust resistance (*Rr*) When the F_1 is crossed with variety A (*rr*), the genes for rust resistance will segregate into two genotypes (*Rr* and *rr*) The wheat plants that are heterozygous (*Rr*), and therefore resistant, can be identified from the susceptible plants (*rr*) by artificially inoculating all plants with stem rust during the seedling stage and noting their rust reaction Only the resistant (*Rr*) plants are then backcrossed to the recurrent parent As many backcrosses may be made as are necessary to obtain plants that are indistinguishable from plants of variety A except for the added genes for rust resistance This may require as many as six or eight backcrosses Since the rust resistant plants selected from the final backcross progeny will be heterozygous for resistance (*Rr*), they must be selfed for one generation to obtain true breeding resistant plants (*RR*) The backcross procedures, as outlined in this example, can be carried out easily since rust resistance is monogenic and dominant, and since the rust resistant plants in each backcross progeny can be identified by artificially inoculating the seedling plants with rust The parentage of the final selection from the above cross might be written "Rust resistant variety B × variety A 5 (or A^5)," to indicate that A was used as the recurrent variety in five crosses

If the genes for rust resistance being transferred to variety A should be recessive (*rr*), the progeny from each of the backcrosses would segregate into two genotypes (*RR* and *Rr*) Since the heterozygote cannot be identified in [illegible] ild be necessary to self the pro [illegible] on to

find resistant (*rr*) plants before backcrossing to the recurrent parent Another possible procedure would be to backcross both the homozygous (*RR*) and heterozygous (*Rr*) plants to the recurrent parent and at the same time self each plant and test the selfed progenies for resistance The backcross progeny from the plants that prove to be heterozygous are then kept, and the backcross progeny from the homozygous plants are discarded If genes for undesirable characters are closely linked with the genes for resistance, they may be added along with the genes for rust resistance The new variety would then be less desirable than the recurrent parent If characteristics being added by the backcross procedure are determined by multiple genes, it may be necessary for the backcross progenies to be grown through the F_2 or later generations to obtain plants that exhibit the desired characteristics before proceeding with the next backcross

In this hypothetical cross, A is a suitable recurrent parent variety, we may assume rust resistance to be inherited as a simple dominant character, and the rust reaction of the backcross derived plants may be determined by inoculation of seedling plants before the next backcross is made A step by step *backcross procedure* is outlined

First year Cross variety A×stem rust resistant variety B

Second year Grow 5 to 10 F_1 plants Backcross F_1 to variety A

Third year Inoculate B_1 plants with stem rust Select 10 to 20 resistant B_1 plants and backcross to variety A

Fourth year Inoculate B_2 plants with stem rust Select 30 to 50 resistant B_2 plants and backcross to variety A

Fifth year Inoculate B_3 plants with stem rust Select 30 to 50 resistant B_3 plants and backcross to variety A

Sixth year Inoculate B_4 plants with stem rust Select 30 to 50 resistant B_4 plants and backcross to variety A

Seventh year Inoculate B_5 plants with stem rust Select 30 to 50 resistant B_5 plants and backcross to variety A

Eighth year Inoculate B_6 plants with stem rust Select 400 to 500 resistant plants to grow the next generation

Ninth year Grow 400 to 500 plant rows Select 100 to 200 rows, homozygous for resistance to stem rust and uniform for variety A plant type Harvest and composite seed

Tenth year Grow in comparison with variety A to determine if backcross derived variety is similar to variety A in all respects other than rust resistance Start increase with remainder of seed As in the preceding example, the number of years required may be reduced if more than one generation of the crop may be grown in the same year Where it is possible to do so techniques need to be developed so that two to three generations may be grown within a year This will reduce the time required to carry out the backcross breeding procedures

One feature of the backcross procedure is that extensive testing of backcross-derived varieties is unnecessary if the recurrent parent type has been recovered However, it appears undesirable to release a variety without some testing to determine that the parent type has been adequately recovered If two or more characters are to be added to a recurrent variety, separate backcross procedures may be pursued for each character and the backcross derived lines from each may finally be merged into a single line

METHODS OF BREEDING CROSS POLLINATED CROPS

The methods used in the breeding of cross pollinated crops, or crops such as cotton and sorghum which have both self- and cross pollination, are not as clearly defined as the methods used in the breeding of self pollinated crops In addition, the methods tend to vary with the particular crop with which the breeder is working The methods of breeding hybrid maize are well adapted to that crop because the location of pollen bearing flowers in the tassel in maize makes possible the easy control of pollination by detasseling and thus the production of hybrid seed on a field scale The use of male sterile lines has to a large extent eliminated the detasseling process and combined with the use of suitable fertility restoring genes, made it possible to adapt this method of breeding to sorghum, onions, and sugar beets It has not been possible to adapt the same method to a cross pollinated forage crop or to cotton, since no practical way of controlling pollination in them has been found In some cross pollinated forage species, such as red clover, incompatibility limits the breeding procedures that can be utilized for their

improvement For these reasons, *methods of breeding cross pollinated species will be discussed at this point only in a broad general way,* so that the problems related to the methods may be contrasted with the methods and problems in the breeding of the self pollinated crops *Specific methods used in the breeding of maize, sorghum, bajra, cotton, and forage crops will be described in detail in the chapters concerning those particular crops* Examples will be cited there to illustrate how varieties are developed by the use of the various breeding methods

The principal methods by which new varieties of cross pollinated crops originate may be classified into four groups (*a*) introduction, (*b*) mass selection (*c*) development of synthetic varieties, and (*d*) hybridization Each of these breeding methods is described

Introduction Introductions may be used as source of new varieties as in self pollinated crops Some varieties are grown as originally introduced Introductions may also be used as sources of desirable genes for disease and drought resistance, quality and other valuable characteristics, which may then be incorporated into adapted varieties by hybridization procedures, or which may be compounded into synthetic varieties

Selection. Selection procedures used in breeding cross pollinated crops differ from those used in self pollinated crops In the self pollinated crops individual plant selections are used to establish uniform, pure line varieties, and mass selection is less widely used as a breeding method But in cross pollinated crops, which are highly heterozygous, individual plants are seldom used to establish a variety for the simple reason that segregation and cross pollination make it difficult to maintain the parent type within the progenies, and a wider range of genetic diversity is generally needed to maintain a vigorous population In cross pollinated crops, *mass selection* is a more common type of breeding than single plant selection Selection procedures more commonly used with cross pollinated crops, in addition to mass selection, include *progeny selection line breeding*, and *recurrent selection*

A MASS SELECTION Mass selection is a selection procedure in which individual plants with desirable traits are chosen and bulked together to grow the following generation It is based on phenotypic selection, that is, on the appearance of the plant and on its particular traits that can be identified. The selected plants are harvested, generally without control of population, and are bulked without benefit of progeny testing

Mass selection was one of the earliest breeding procedures with cross pollinated crops It was the principal breeding procedure with open pollinated maize and was practiced by the American farmer when he selected ears for planting the next crop Mass selection has been practiced in breeding forage crops, sugar beets, cotton, and other crops

Although selection is based on the phenotype, its purpose is to obtain a greater frequency of superior genotypes within the population The effectiveness of mass selection is dependent upon the accuracy with which the phenotype reflects the genotype Mass selection has been effective in sorting out and accumulating genes for particular quantitative characters which can be seen or measured easily and which can therefore be used as the basis for selection In open pollinated maize it was possible to develop varieties changed in earliness of maturity, height of plant, size of ear, type of indentation, percentage of oil, and similar characteristics by continuous mass selection It is necessary that genes for these differences exist within the mixed population if mass selection is to be effective Granted that the necessary heritable variations are present, the rate of progress is more or less dependent upon the ability of the breeder to pick plants genotypically different as well as differing in phenotype Mass selection has been less effective in improving characters like yield, which fluctuate greatly with the environment and which cannot be accurately identified by the phenotype

The principal advantage of the mass selection method of breeding is its simplicity and the ease with which it can be carried out It is relatively simple for the breeders to select and composite seed from what appear to be phenotypically superior plants Also, new varieties can be developed rather quickly Since the improved strain will not differ greatly in range of adaptation from the parent variety, less time is required for testing than with new breeding materials

The breeding progress that may be made by mass selection is limited to the range of genetic variability already present in the population Since selection in naturally cross pollinated crops is

based on the maternal plant only, there is no control of the pollen par nt or the genes it contributes to the progeny Also, it is not possible to distinguish between plants phenotypically superior owing to the environment from those superior owing to heredity

In addition to its use in breeding new varieties, mass selection may be used to maintain purity in varieties of cross pollinated crops Mass selection was a common method of maintaining seed stocks of open pollinated maize It has been used extensively to maintain varietal purity in cotton, although it has now largely given way to some system of progeny testing in this crop

B PROGENY SELECTION AND LINE BREEDING *Progeny (plant to row)* selection is a procedure in which progenies are grown in individual plots in order to determine the breeding behaviour of selected plants By the progeny test plants whose superiority is due to genetic variation may be distinguished from plants whose superiority is due to the environment In cross pollinated crops individual plants are more or less heterozygous, and the progeny will segregate for the heterozygous characteristics By growing a progeny of twenty five to fifty plants the range of variability of any particular line may be established Progeny selection is most easily carried out with crops that may be evaluated and harvested as individual plants such as cotton, jute, sunflowers, and castor Progeny selection is more difficult with crops such as forage grasses and legumes, which grow in dense stands so that individual plants are hard to separate

With progeny selection open pollinated seed may be harvested from selected plants, or pol lination may be controlled in some manner so that selfed seed may be harvested Selfing tends to fix characters in a pure form since self pollination leads to homozygosity This is desirable in the case of a character such as disease resistance, early maturity, leafiness in a forage species, or other characteristics used as the basis of selection Inbreeding leads to a reduction in vigour in cross pollinated species The rapidity with which vigour is lost after self pollination may determine the number of generations that inbreeding may be practiced in a system of progeny selection before outcrossing with other strains is needed to restore vigour Inbreeding may be limited in cross pollinated crops which possess incompatibility alleles and do not set seed freely after self pollination Although the seed set after self pollination in crops with incompatibility alleles may be small, it is often sufficient to maintain the strain

Varieties of cross-pollinated crops are seldom developed from the progeny of a single plant because inbreeding reduces vigour More commonly a group of progeny lines which are similar in phenotype is composited This procedure, as used with cotton or sugar beets, is sometimes referred to as *line breeding* Various modifications of the procedure are practiced by different breeders For example each group of phenotypically similar lines may be grown in isolation and open pol lination permitted within the group This procedure helps to maintain the vigour that might be lost by more rigid control of pollination

C RECURRENT SELECTION Recurrent selection is used with cross pollinated crops to concentrate genes for a particular quantitative characteristic in a population, without a marked loss of genetic variability The characteristic under consideration should be one that can easily be recognized by the phenotype Recurrent selection has been used to improve oil content in maize, fibre strength in cotton, sugar content in sugar beets, and other characteristics of a similar nature The procedure is to select from a mixed population plants that are superior for the character under consideration The plants are selfed and the selfed seed is used to grow plant to row progenies (Fig 4 5) The plant to row progenies are then crossed in all possible combinations Hybrid seeds from these crosses are composited and a bulk population is established to start the first recurrent selection cycle From the bulk population, plants superior for the character under consideration are again selected and used to establish new plant to row progenies The plant to row progenies are crossed in all possible combinations as before The hybrid seed is com posited to grow a bulk, which is used to start the second recurrent selection cycle The process may be repeated as long as improvement is shown in the character being selected (Fig 4 6) [22]

Compounding Synthetic Varieties Synthetic varieties are used for the improvement of forage crops, sugar beets, maize, and other cross pol linated crops Many new varieties of forages are being developed by compounding seed of individual plants, or strains, into a synthetic variety The

synthetic varieties may range from mixtures of seed harvested from a few carefully selected plants to a uniform blend of seed from several distinctly different strains, inbred lines, or clones

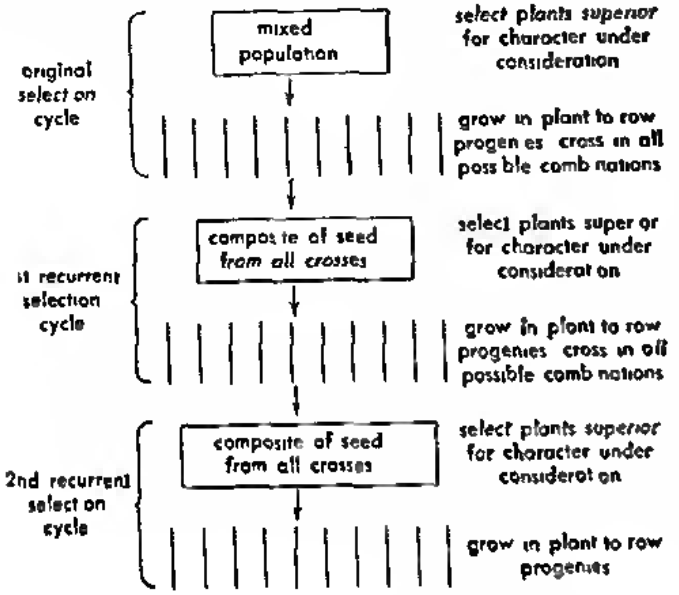


Fig 45 Recurrent selection is a selection procedure designed to concentrate genes for a particular quantitative character and still maintain a broad genetic base Plant to-row progenies from superior plants are crossed in all possible combinations and the hybrid seed is composited This population is then used to start a new selection cycle

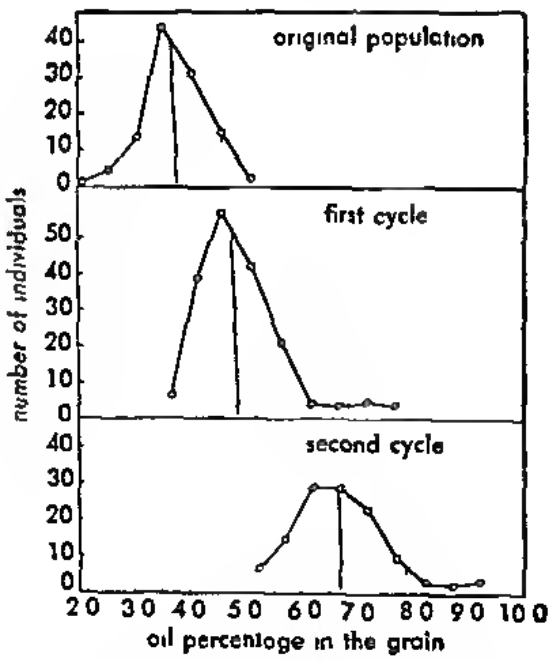


Fig 46 Comparison of oil percentage in a synthetic population of maize after one and two cycles of recurrent selection After Sprague, Miller and Brimhall [22]

Before deciding how the synthetic is to be compounded, the performance of the resulting hybrid combinations is tested Only plants or strains with superior hybrid combinations are then put into the synthetic This procedure distinguishes a synthetic from a simple mass selection, in which seeds of plants, or strains, are bulked without previous testing of progeny performance or performance of the hybrid combination It also distinguishes a synthetic from line breeding in which progenies are grown and established lines are composited on the basis of progeny performance of the lines *tested individually* Many complex procedures may be used to evaluate the combining ability of specific plants, or strains, in order to determine which will give the most productive combinations Some of these will be discussed in the chapters dealing with the breeding of maize, and forage crops In a synthetic variety, the original breeding material is usually kept viable so that the synthetic may be reconstituted at any time

The development of synthetic varieties has been suggested as a method of breeding maize With maize, the procedure is to intercross a large number of inbred lines or plants, and then to grow the bulk population for several generations The synthetic can be reconstituted at any time by crossing the inbred lines again and thus starting a new bulk population Synthetic varieties do not yield as high as the best F_1 hybrids between the inbred lines, but they are superior to the open-pollinated varieties of maize from which the inbred lines were derived

Hybridization. Two basic hybridization procedures are used in the breeding of cross-pollinated crops These involve *intervarietal* or *interspecific crossing* and *utilization of hybrid vigour*

A INTERVARIETAL AND INTERSPECIFIC CROSSING Crosses between varieties, or between species, may be used to combine genes for desirable characteristics from different parents, as with self pollinated crops In cross pollinated crops, each plant may itself be an individual hybrid, in which case segregation will occur within the F_1 generation Hybrid plants in the progeny of the cross, if pollination is uncontrolled, will in turn cross freely with other hybrid plants within the population so that the progeny from the cross is not resolved into homozygosity as with self-pollinated crops For this reason, after hybridization selection procedures will

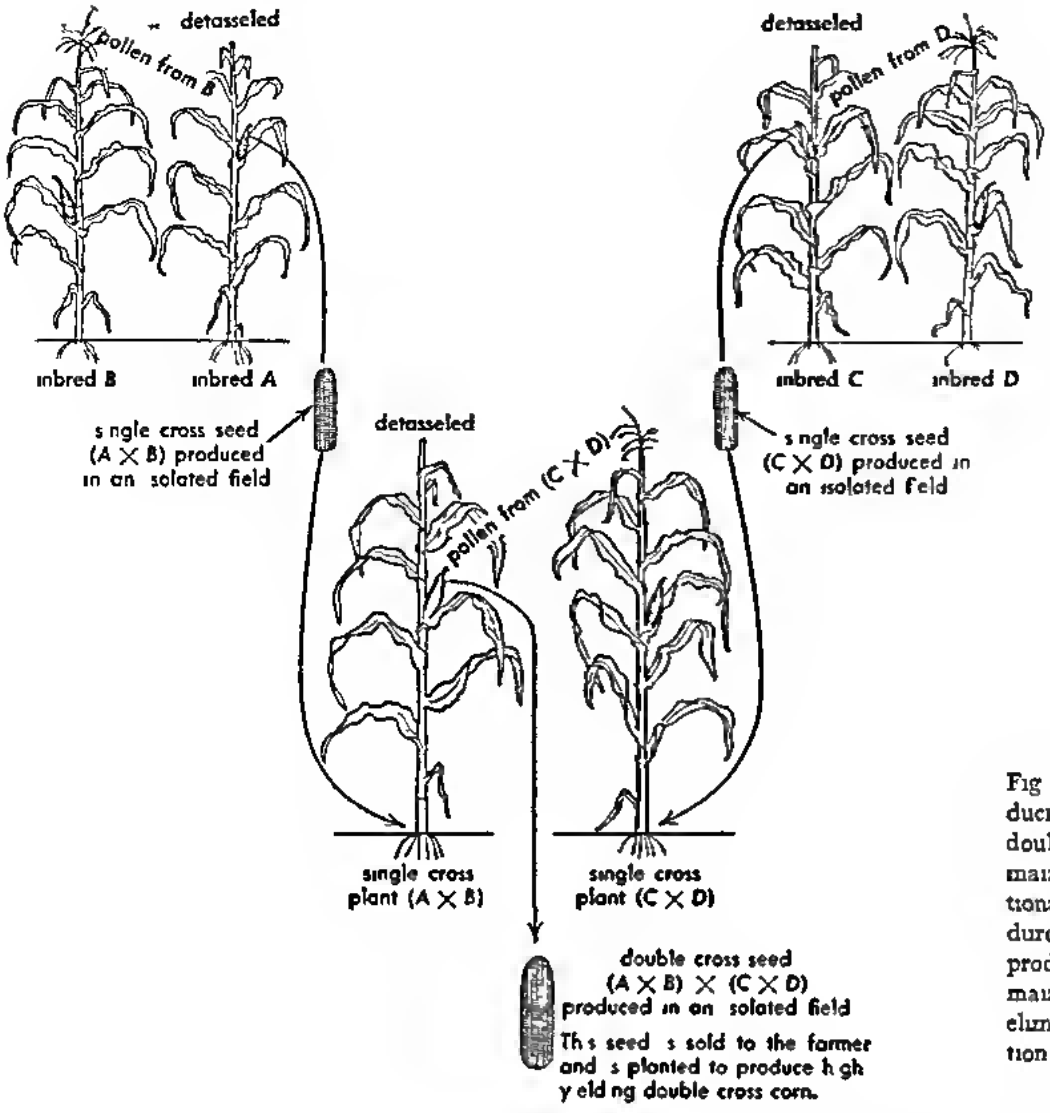


Fig 4 7 Method of producing single crosses and double crosses of hybrid maize by the conventional detasseling procedure In the commerical production of hybrid seed maize detasseling is often eliminated by the utilization of cytoplasmic male sterility

differ from those used with self pollinated crops Phenotypically desirable hybrid plants will usually need to be selfed for one or more generations to fix the desirable characters in a homozygous condition From the hybrid population, by progeny selection lines are then established which combine the desirable characteristics of the parent varieties Some form of outcrossing the selected lines eventually may be necessary to restore the vigour lost during inbreeding

B UTILIZATION OF HYBRID VIGOUR It is common observation that the F_1 generation in many crosses is more vigorous than the parent stocks The increase in vigour, growth, size, yield, or function of a hybrid progeny over the parents is known as *hybrid vigour* or *heterosis* A breeding system based on the utilization of hybrid vigour was first applied successfully to the development of hybrid maize Hybrid vigour is now utilized also in the breeding of sorghum, bajra, wheat, onions, tomatoes, cucumbers, and many other field and vegetable crops To utilize hybrid vigour, uniform F_1 populations are produced in such quantities that the F_1 seed can be grown directly

As applied to breeding hybrid maize, the utilization of hybrid vigour involves three steps (Fig 4 7) (*a*) production of uniform homozygous inbred lines, (*b*) crossing inbreds in combinations that give uniform and productive *single cross* (F_1) hybrids, (*c*) crossing single crosses in combinations to give productive *double cross* hybrids In other crops the single cross is grown by the cultivator and a double cross is not produced

This method of breeding is based on fundamental knowledge about the inheritance of maize The inbreds are stable for morphological and physio

logical characteristics Although vigour is lost during the early generations of inbreeding (Fig 3 8), the inbred lines become stabilized about the F_7 to F_8 generation, and *no further loss of vigour* is experienced, so that the geno ype may be maintained indefinitely The F_1 hybrid is obtained by crossing inbred lines chosen for their ability to mate with other inbred lines and to produce a vigorous and productive hybrid progeny The cross between the F_1 hybrids, or single crosses, is made so that seed can be harvested from a vigorous F_1 plant This makes possible the abundant production of hybrid seed and thereby lowers the cost of the seed to the cultivator The procedures for breeding hybrids are described in more detail in the chapters on breeding wheat, maize, sorghum, and millets

The procedure of producing hybrid maize as originally devised, *involves* detasseling the female parent inbred lines (Fig 4 7) and permitting open cross pollination in isolation In commercial hybrid seed production, utilization of cytoplasmic male sterility has eliminated much of the work of detasseling the female parent lines By utilization of cytoplasmic male sterility, the scheme of hybrid seed production used with maize has been extended to sorghum, bajra, wheat, onions and other crops The utilization of hybrid vigour is not restricted to the F_1 of crosses between homozygous plants, but may be exhibited also by the F_1 of crosses between heterozygous plants In asexually propagated crops such as sugar cane, the F_1 hybrid plant may be propagated by vegetative means without the necessity of producing hybrid seed on a commercial scale This procedure was utilized in the U S A in the propagation of the Coastal variety of Bermudagrass The Coastal variety originated as a vigorous hybrid plant in a cross between two strains of Bermudagrass

METHODS OF BREEDING ASEXUALLY PROPAGATED PLANTS

Asexual propagation is used with species that produce seeds very poorly, or that produce seeds only under special conditions Some crops normally progapated asexually are sugarcane, potatoes, tea and certain varieties or species of grasses Plants propagated asexually are normally highly heterozygous Procedures for breeding asexually propagated plants are (*a*) clonal selection and (*b*) hybridization

Clonal Selection. Clonal selection may be practiced in mixed populations of asexually propagated species By this procedure superior clones may be isolated from the population Selection in mixed populations is based on the phenotype The genotype of the superior clone is then maintained by asexual propagation Progress by clonal selection is limited to the isolation of the best genotype already present There is very little opportunity to improve the heredity of a variety propagated asexually Vegetative propagation maintains the genotype without change, unless mutations occur and produce bud sports chimeras, or genetic mosaics Beneficial mutations of this type occur relatively infrequently

Hybridization. Gene recombinations occur only as a result of sexual reproduction In this group of plants, sexual reproduction is thus used to create genetic variability By increasing a large number of clones, selected as parents because they possess superior characters new populations will be created The hybrid progenies are used then as a source for the selection of new clones Since the parent clones will be heterozygous, segregation will occur in the F_1 generation Each F_1 plant is thus a potential source for a new clone If the breeder does not find the particular recombination for which he is looking, the crosses are remade, or new crosses may be made Selfing to produce an F_2 is seldom practiced as selfing may lead to a reduction in vigour, which would be undesirable Superior plants from the hybrid progenies are propagated vegetatively to establish a clone The clone may then be tested for yield and other characteristics in replicated plot tests Genetic purity is easily maintained with vegetatively propagated plants and large numbers of strains or varieties can be grown together in the breeding nursery

Wide crosses are sometimes made to bring in desirable characteristics, such as disease resistance, from related species The F_1 plants from the wide crosses may be less desirable from an agronomic standpoint, on account of the presence of undesirable genes inherited from the wild species These undesirable genes can be eliminated by successive backcrosses by using the cultivated species as the recurrent parent Since backcrossing is a form of inbreeding, successive backcrosses to the same cultivated variety may lead to reduction in vigour In sugarcane, two or three different

cultivated varieties are sometimes used as recurrent parents The backcrosses are then made successively first to one and then to another of the cultivated varieties

The breeding procedures for asexually propagated crops will be illustrated more fully in Chapter 12 on Breeding Sugarcane and in Chapter 13 on Breeding Potato

NEW BREEDING TOOLS

The methods of breeding already described deal largely with finding strains or plants with superior combinations of genes in existing populations and increasing them into agricultural varieties, or with the creation of mixed genetic populations by artificial hybridization from which superior genotypes may be selected It is by these conventional breeding methods that most new agricultural varieties have been developed in the past The extent to which a particular crop can be improved by these methods of breeding is limited by the amount of variability within the species and its availability to the breeder The purpose of building large world collections of the different agricultural crops and maintaining them in a viable condition is to make available to the breeder a greater variety of genetic stocks These collections may then be searched for desirable genes, such as lodging resistance or resistance to a certain disease, as the need for such genes arises in a breeding programme

In the evolutionary process which plants undergo in nature, gene recombination by natural hybridization plays an important part in increasing the variability within a species Two other natural forces which increase variability are (*a*) mutation and (*b*) polyploidy

The importance of mutation and polyploids in the evolution of plant species has long been known But it is only in recent years that means have been available for the practical plant breeder to create at will and utilize mutations or polyploids for the development of improved agricultural varieties The knowledge that radiations and chemical mutagens will increase the mutation rate in a crop species has led to the development of a new breeding procedure, sometimes referred to as *mutation breeding* As a tool of the plant breeder, mutation breeding is yet in the developmental stage The discovery that *polyploidy* can be artificially induced by the use of colchicine and other means has stimulated the practical breeder to utilize variants created by doubling chromosome numbers, or by combining chromosome sets from species hybrids, as sources of new breeding materials

Mutation Breeding. It has been known since 1928 that mutations may be induced in plants by various forms of radiation [23] This knowledge led to the extensive use of radiation-induced mutations in genetic studies with plants Reports of experiments in Sweden[8] in which mutations for straw stiffness, earliness quality, and other agronomically useful characters in barley had been induced by x rays stimulated interest in the possible use of radiations as a tool of the practical plant breeder as well as the theoretical geneticist Atomic investigations have made available new and powerful sources of radiations which are also being investigated in attempts to find mutations useful in crop improvement The method of breeding is based on the principle that the rate of mutation can be increased by exposure of the plant or seeds to radiations Since useful mutations are produced in nature, it is assumed that valuable mutations also may be produced experimentally

The common procedure with this type of study is to irradiate dry seeds with x-rays or atomic radiations known as thermal neutrons or to treat with chemical mutagens Treated seed is generally reduced in germination, depending upon the reaction of the particular species and variety and upon the severity of the radiations Seedling plants grown from the treated seed may vary from very weak to normal in appearance The mutations are usually carried in sectors of plants in the generation following radiation (Fig 3 9) so the R_1 (first generation after exposure to radiations) plants are generally harvested by tillers or branches The R_2 generation is then studied to find plants which have segregated desirable mutant characters Some of the common mutations observed which may be beneficial to the breeder include shorter straw, higher yield, larger kernels, early maturity, and disease resistance [6 7 9 21] Selected mutant plants are harvested and planted in progeny tests in the R_3 and in later generations for evaluation of the mutant characters

Some of the limitations of radiation breeding were listed in Chapter 3 How extensively breeders will utilize radiation or chemical induced mutations is not yet fully determined

Polyploidy. Many crop species are natural polyploids, i e their chromosome number has been increased by multiples of the haploid number They include common cultivated crop species such as wheat, oats, cotton, tobacco, and many forage grasses and legumes Characteristics of natural polyploids are larger size, increased vigour, and greater productivity This fact has suggested to breeders the possibility of increasing the yield of plants of a particular species by artificially doubling or otherwise increasing the chromosome number

Artificial polyploids of almost all of the common crop plants have been produced at one time or another [4 16] In general, these polyploids have been larger in size than the corresponding diploids, probably as a result of the increased cell size which generally accompanies the increase in chromosome number Other changes in plant structure usually associated with polyploidy are thicker and stouter stems, broader and thicker leaves and larger fruits and seeds Few if any of the newly produced or raw polyploids are immediately useful in agriculture They possess certain defects which must be corrected by further breeding before they are superior to the corresponding diploid Different crop species differ in their response to polyploidy [5 16 19 24] Rye red clover, white clover, alsike clover, and sugar beets offer promise of being adapted to this type of breeding Polyploids of soybeans, linseed, and maize, on the other hand, have been quite inferior In general, *plants with low chromosome numbers* respond more favourably to chromosome doubling than plants with high chromosome numbers *Crops grown for their vegetative parts* rather than for seed appear to be better suited for polyploidy breeding since chromosome doubling tends to increase plant size but has a deleterious effect on seed production *More success has been attained with cross pollinated crops than with self pollinated crops*, since there are more possibilities of desirable recombinations with cross pollination

A good example of successful polyploidy breeding is the variety of rye known as Tetra-Petkus (Fig 4 8) Tetra Petkus rye was produced by doubling the chromosome number of a European variety Tetra Petkus rye is an exception to the generalization made above that crops grown for their seed are unsuited for polyploid breeding, but does fulfill the other two requirements The fertility

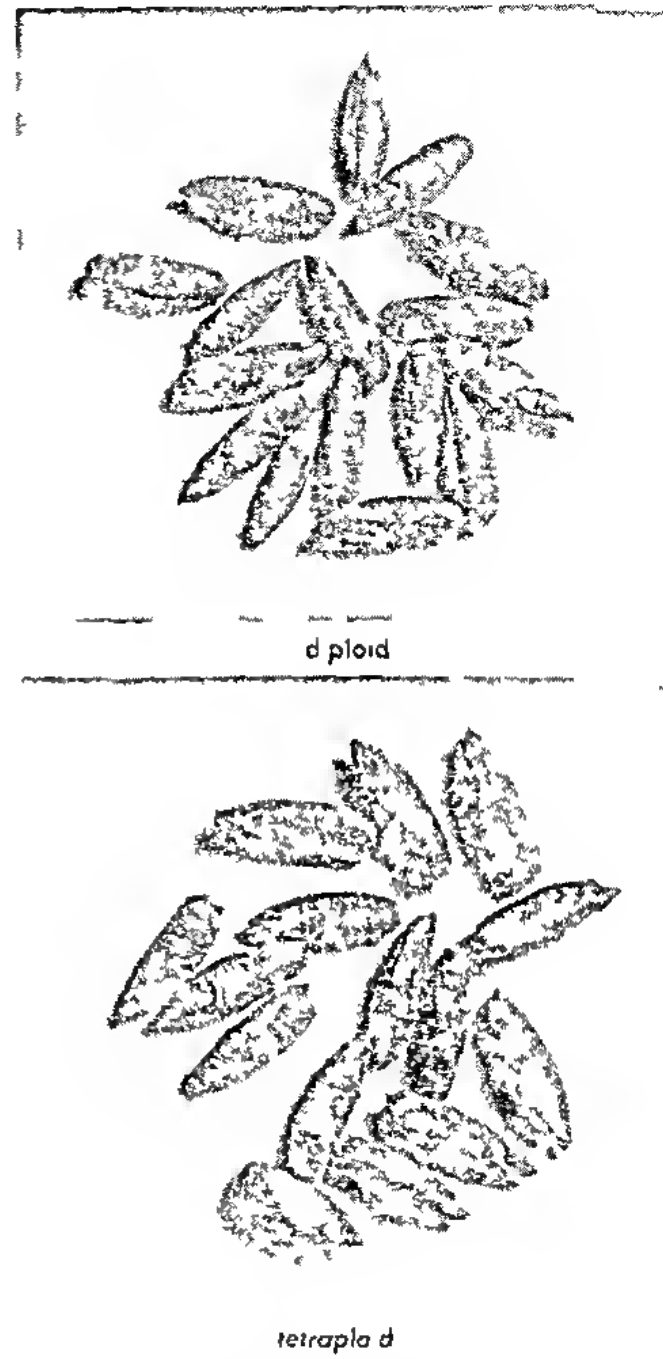


Fig 4 8 Seed of a d ploid variety of rye, Balbo, and a tetraploid variety Tetra Petkus

of Tetra Petkus rye is reduced if permitted to cross pollinate freely with a diploid variety Progress in the breeding of tetraploid strains of red clover have been reported from Sweden [16] Tetraploid strains of berseem have been developed at the Indian Agricultural Research Institute Different plants of these crops respond differently to polyploidy As a result, it is a to d chromosome number er

and then to start, at the tetraploid level, a new breeding programme with conventional methods of selection and gene recombination Another type of polyploid which has received much attention was derived from rye wheat crosses [19] Known as *Triticale*, the rye-wheat contains 42 chromosomes derived from wheat and 14 chromosomes derived from rye for a total of 56 chromosomes Polyploidy has been used in some countries to improve the sugar beet In sugar beets the triploid has been the most productive state of ploidy Tetraploids of sugar beets are produced and crossed to a diploid to produce the triploid

TESTING EXPERIMENTAL STRAINS

A plant breeder deals with many thousands of experimental strains Only occasionally will one of these strains possess a combination of characteristics sufficiently superior to those of commercial varieties already being grown to justify its being increased, named, and distributed as a new variety It is the job of the plant breeder not only to create and isolate new strains by the various breeding procedures but also to recognize and identify those that are superior This he does by careful observation of their performance in as many ways as possible, and by employing rigid testing procedures in which the experimental strains are compared with superior commercial varieties Many techniques may be employed as part of the testing procedures These will be discussed in more detail in the following chapter Strains may be tested for disease resistance by subjecting them to artificially induced epiphytotics of the disease, either in the field or in the greenhouse By the use of freezing chambers plants may be subjected to cold tests to measure their winter hardiness Quality of the grain may be established by suitable chemical and physical tests Ultimately each new strain must prove its worth in the field in carefully conducted yield tests *From three to five years of yield testing, in which new strains are compared with the best commercial varieties over a wide range of soils and climate in the area where the variety is to be grown, are generally considered necessary before a strain should be increased and distributed as a new variety*

Seldom does a breeder have the means to test new strains in the field as widely and extensively as desired To assist in the testing of promising new hybrids of maize and sorghum in the various production areas in south and southeast Asia, coordinated maize and sorghum improvement schemes have been formed Maize, sorghum, and bajra hybrids developed in the breeding programme are supplied to all of the states of India and to countries in southeast Asia for testing This enables agricultural experiment stations in all of the maize and sorghum producing areas to receive the latest developments of the plant breeders Breeding materials are also exchanged with the International Maize Improvement Programme, Mexico, and with certain countries in the middle East and Africa This international cooperation and collaboration should prove useful in the advancement of maize and sorghum improvement in all of the countries concerned By pooling their efforts and germplasms greater progress may be achieved with limited available resources Similarly, new strains of wheat and rice are tested in the different states of India through All India Co-ordinated Wheat and Rice Improvement Projects

INCREASING, NAMING, AND DISTRIBUTING NEW VARIETIES

When a strain with superior performance has been developed, it may be increased, named, and distributed as a new variety In the early stages of selection only a small amount of seed is generally available Often this will not exceed a few grams if the strain originated from a single plant. This small seed supply must be increased through successive generations until an adequate amount is on hand to distribute widely to the cultivators, who may require several hundred or several thousand tonnes, depending upon the specific crop, the anticipated demand for the new variety, and the system of distribution From this small beginning of a few grams of seed harvested from a single plant, the breeder normally proceeds to a plant row, to preliminary yield tests and disease nurseries, to replicated yield tests, and finally to advanced plot tests By the time that a strain has been advanced through several years of field testing and sufficient information about the strain is available to make a sound decision regarding its being named and distributed, the seed supply will normally range from a few kilograms to several quintals This supply of seed is multiplied further to accumulate the amount needed for final distribution Since a certain amount of mixing or natural

crossing will inevitably occur when large numbers of strains of a self pollinated crop are handled in adjacent rows in the breeding nursery, purification of the variety is usually necessary before final increase is made Purification may be accomplished by roguing out off type plants, by growing large numbers of plant to row selections, or by other means In rice, a plant grown from a single seed can be divided and redivided in the tillering stages so that large quantities of seed can be produced in one season from the vegetatively propagated offsprings This helps in maintaining the purity of the type as well as enables the breeder to get the maximum increase of seed from a small initial stock Final distribution may sometimes be speeded up by making preliminary increases of outstanding strains before the final testing is completed, and by taking the seed to other areas of the country where an extra crop may be grown during the winter season

Before release from a breeding station, a new variety is given a name by the originator The name may be a word, a number, or a combination of words and numbers

In India each state has a variety release committee The names of the varieties approved by the state committee are forwarded to the Central Variety Release Committee at the Indian Council of Agricultural Research New Delhi, for registration of the varieties The purpose of registration is to provide an authentic record of the new variety and a description of its characteristics

Distribution of the varieties are generally made through the state research stations Recently the Central Government has sponsored the formation of a National Seeds Corporation for the purpose of distribution of pure seeds on an All India basis

Procedures for seed increase and distribution are discussed more fully in Chapter 18 on "Seed Production Practices"

THE ART OF PLANT BREEDING

Selection is an intrinsic part of plant breeding, it is as old as plant breeding itself Whenever the breeder chooses between plants or strains to grow and those not to grow, he is practicing selection With thousands of plants or strains to choose between, his reasons for making a particular choice should always be clear Usually the breeder has in his mind a distinct picture of the type of plant he wants to find In making the choice the wise breeder exercises skill and judgement gained from experience and knowledge about the plant with which he is working *This is the art of plant breeding* The clarity and precision with which he can evaluate a strain may be enhanced if his visual observations are supplemented with accurate information about the performance of the strain, which has been obtained through various testing techniques For this reason a large part of the breeder's work is devoted to 'testing" procedures designed to help him evaluate the breeding materials Some of these procedures are discussed in the following chapter Their employment is a necessary part of his work, as they supply him with accurate and specific information about the performance of the strains he is growing But their usefulness ends there The tests cannot weigh the merits of individual plants or strains and decide which to keep and which to discard Only the breeder can do that.

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5

Techniques in Breeding Field Crops

In all fields of science, the experimenter develops special skills, procedures, and techniques which he uses in the pursuit of his research [a] In this respect the plant breeder is no exception In the practice of plant breeding, the breeder (*a*) finds or creates genetically mixed populations of plants, (*b*) selects strains with desirable characteristics from the mixed populations, and (*c*) tests the selected strains in pure lines or in combinations to determine if they possess the characteristics for which he is looking in the desired intensity

When a superior strain or combination of strains has been isolated and identified, it is increased for commercial distribution as a new variety Before the breeder finds a strain with sufficient merit to be increased and distributed, it is generally necessary for him to make many crosses and to grow many thousands of experimental strains The careful evaluation of so many strains is a huge task, and generally consumes the greater portion of the breeder's time, as well as the funds and facilities at his disposal To avoid waste and inefficiency in his breeding programme, it is mandatory that the breeder develop careful and accurate crossing and selection techniques and use efficient and thorough procedures for testing the breeding materials

The testing of strains is carried out both in the field and in the glasshouse Field tests are generally preferred because they are usually more economical and more nearly approximate farm conditions Evaluation of strains for some characteristics, like yield and adaptation, can be done only in the field (Fig 5 1) Glasshouse tests are just as satisfactory or even superior for certain types of tests, and they may enable the breeder to evaluate strains for certain specific qualities, or advance some breeding materials one or more generations during the winter months if he cannot grow it satisfactorily in the field at that time (Fig 5 2A) For this reason a glasshouse is an indispensable aid to the plant breeder in cool climates In addition to the glasshouse, a screenhouse is also useful, in order to give protection from birds or rodents, or insects that may carry plant diseases or that may perform unwanted cross pollinations (Fig 5 2B) In the warm climates, as in most of south and southeast Asia, the screenhouse may be used throughout the year In addition, the breeder will need to have at his disposal a small acreage of land, suitable in fertility, drainage, and topography for the specific crop with which he is working The amount of land needed will be determined by the particular crop and the extent of his breeding programme Less land is required to grow a given number of strains of closely spaced crops, like wheat or rice, than is needed for widely spaced row crops, like maize, sorghum, or cotton Soil should be as uniform in all respects as it is possible to obtain and representative of the area where the variety is to be grown Soil with high fertility is desired in order to obtain optimum yield differences between strains, particularly when selecting for response to high fertility or if evaluating lodging resistance, although differences in winter hardiness, disease and insect resistance, and other characteristics may sometimes be obtained more satisfactorily at lower fertility levels High yield per se is not the measure by which the breeder evaluates a new strain, superiority is determined by the *comparative yield* (or other characteristics) *of the new strain in relation to that of the best commercial variety* grown in as nearly identical conditions as possible For this reason some adapted commercial variety, or experimental strain, with well known characteristics, is always grown under similar conditions, treated in a similar manner, and

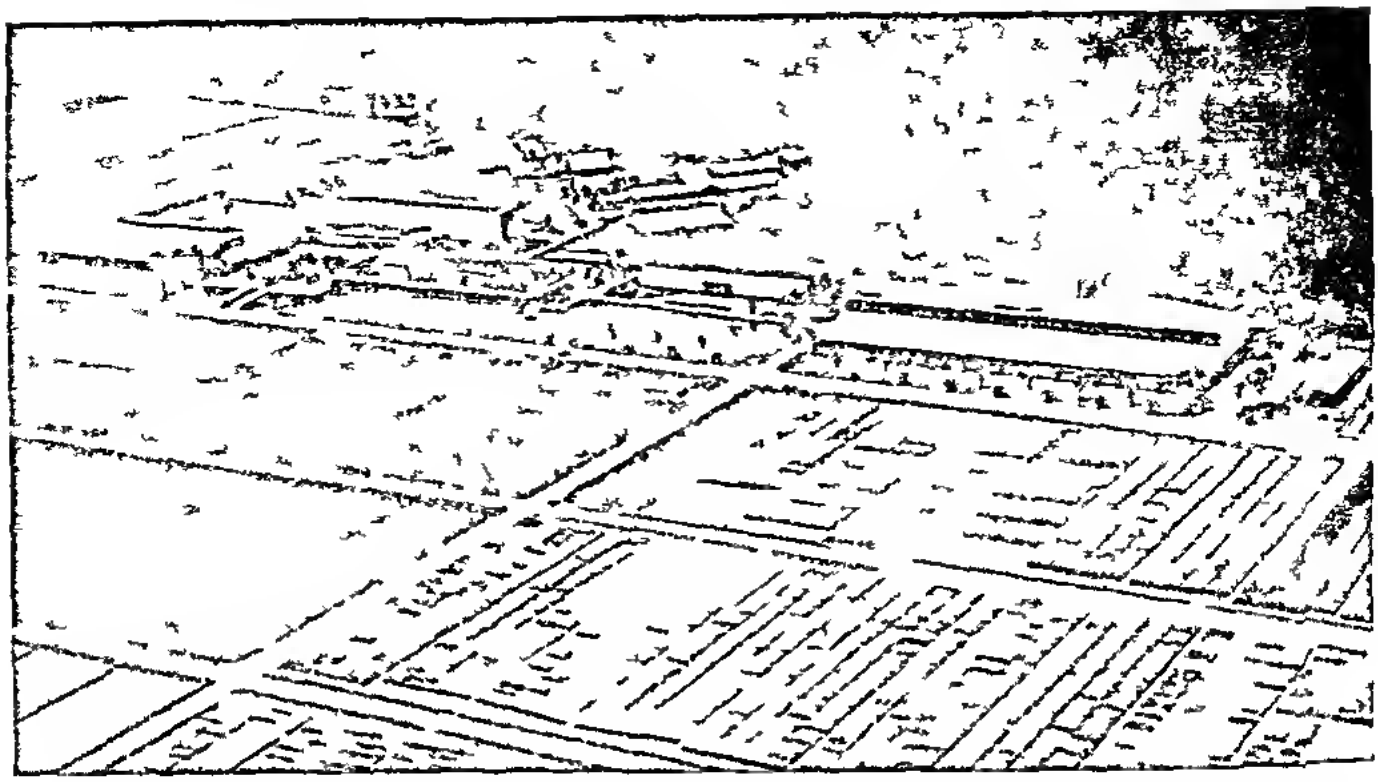


Fig 5 1 Aerial view of the International Rice Research Institute Los Banos Laguna Philippines with the rice breeding nursery plots in the right foreground The breeding nursery is the plant breeder s laboratory where he observes the performance of new strains and evaluates the characteristics important in their breeding

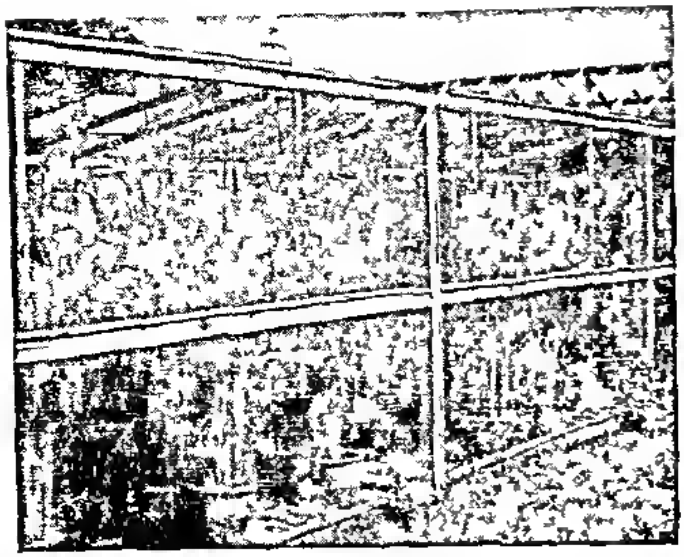
used as a check variety for comparison with the experimental strains in all testing procedures

In the conduct of a testing programme it is frequently necessary to develop special equipment for planting harvesting threshing ginning or measuring special features and quality characteristics A resourceful breeder according to his specific problems will use many techniques which enable him to obtain more accurate data Some techniques and procedures are more or less standardized and are used by many breeders General descriptions of some of the more widely used techniques and the principles in their application to the breeding of field crop plants will be described in this chapter Specific techniques that are used only with special crops will be referred to in the chapters concerning those crops

SELFING AND CROSSING TECHNIQUES

Selfing and crossing are essential procedures in breeding crop plants It is important that the breeder master these techniques in order that he may manipulate the pollination according to his needs The exact procedures that he may use to ensure self or cross pollination of specific plants will depend upon the particular species with which he is working the structure of the flowers in the species and the normal manner of pollination For this reason it is essential that the breeder thoroughly acquaint himself with the flowering habit of the crop If this information is unknown he may need to spend some time studying the crop to obtain

5 2A



5 2B

Fig 5 2 A Glasshouse at the Indian Agricultural Research Institute New Delhi The plant breeder uses the glasshouse for crossing growing early generations of hybrid progenies testing strains for disease resistance and many other purposes B Screenhouse at Central Rice Research Institute Cuttack The screenhouse protects experimental plants from birds and other pests

this knowledge before developing an extensive breeding programme

Selfing Selfing or inbreeding of *self* pollinated species offers no particular problem to the breeder In them, the plant is permitted to follow its normal mode of pollination and the seed is harvested This is the procedure used with wheat, rice, barley, pulses, soybeans, groundnuts and similar crops when making plant or panicle selections It is important that the breeder know something about the extent of natural cross pollination within his breeding material If slight, this natural cross pollination may be ignored in normal breeding procedures The breeder may depend upon segregation bringing to light the strains that originate as the result of cross pollination, and at that time be may eliminate them But *if natural crossing is excessive, or if precise results are desired*, it may be necessary to protect the flower by bagging or other means to prevent foreign pollen from reaching the stigma

In the selfing or inbreeding of cross pollinated species it is essential that the flower be bagged or otherwise protected to prevent natural cross pollination In the cross pollinated species of grasses, which are normally pollinated by wind blown pollen, bagging the heads with parchment or glass ine envelopes is a common procedure It is usually necessary to shake the bagged heads daily until flowering is completed to disseminate the pollen Seed set is frequently reduced in heads enclosed in bags, probably because of the excessive temperature inside the bag In crops like cotton which have large flowers, the petals may be folded down over the sexual organs and fastened, and thereby pollen and pollen carrying insects may be excluded Hand tripping in addition to bagging is generally necessary in many legumes to obtain self pollination In certain legumes which are almost entirely insect pollinated the plants may be caged to exclude the insects In maize a bag is placed over the tassel to collect pollen, and the shoot is bagged to protect it from foreign pollen The pollen collected in the tassel bag is then transferred to the shoot

Emasculation Practices Knowledge of cross ing procedures is extremely important to the plant breeder since hybridization is one of the principal methods of breeding crop plants Crossing is generally accomplished by removing the stamens from the seed parent, a process known as *emasculation* The stigma is then pollinated with pollen collected from the pollen parent Various techniques[19 23 29] have been devised to facilitate emasculation and pollination

Emasculation is unnecessary in monoecious or dioecious crops With them, it is necessary only to protect the pistillate flower before the stigma ripens and becomes receptive from foreign pollen until it is pollinated by the breeder with pollen collected from the desired source With bisexual flowers, *emasculation of the seed producing flower is completed* before the anthers ripen and self pollen reaches the stigma (Figs 5 3, 5 4), or emasculation is circumvented by some procedure that will permit an acceptable degree of cross pollination Some of the emasculation procedures commonly used by breeders are described

1 *Removal of the anthers* Anthers may be removed with the aid of forceps, suction, or other means, before pollen is shed This is the most common method of emasculation with wheat, rice, barley, oats, grams, soybeans, grasses, cotton, linseed, sugar beets, tobacco, and many other crops Small forceps with thin, rounded points are desirable (Fig 5 5) For soybeans, grasses, and other crops with extremely small flowers, forceps with fine points are required [5] Fine ' forceps or small

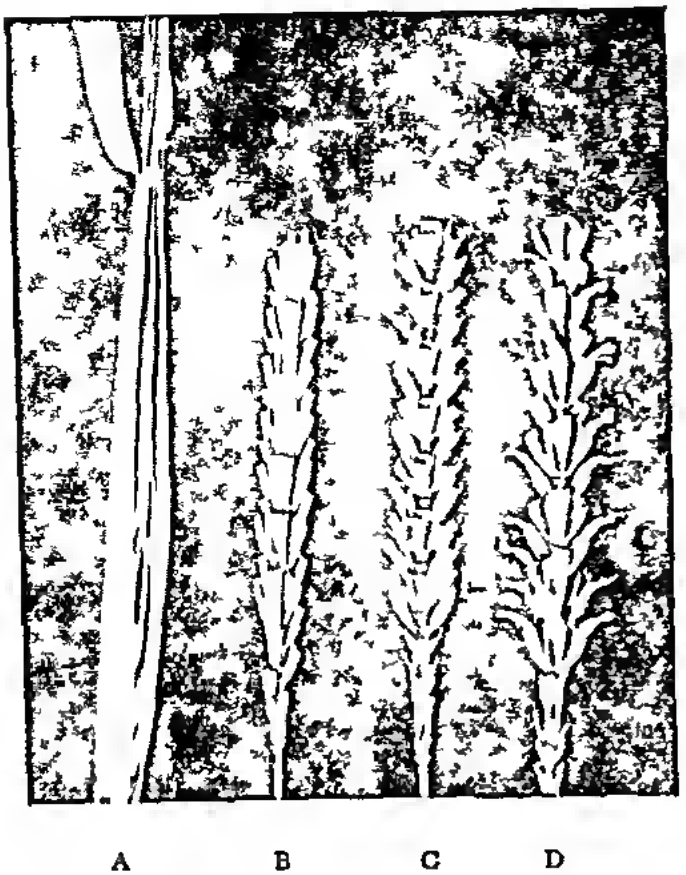


Fig 5 3 Barley sp kes selected to show successive stages in emasculation and crossing A Sp ke at the stage of develop ment when emasculat ons are normally made in barley B Sp'ke after emasculation The glumes have been cut back to facilitate emasculation and pollination Note that the im mature florets are closed C Spike at a des rable stage for poll nation Note that the florets are now open D Set of seed obtained from crossing

Fig 5 4 After emasculation head bags are slipped o er the barley spike to prevent natural cross-pollination and are held in place with small cl ps After cross ng a tag is attached to show the parents and the date of the cross

bent hooks are sometimes used with small flowered legumes Suction has been used successfully to emasculate small flowered legumes [23] [33] A small, pointed instrument or a lead pencil may be used to roll out the anthers of linseed and sugar beets Anthers of tobacco may be plucked off by hand

2 *Killing the pollen by heat cold or alcohol* Hot water has been used to kill pollen in sorghum [39] rice[20] and grasses, [21] [22] and thus the removal of anthers is unnecessary The flowers are immersed in hot water with temperatures ranging from 45 to 48 degrees centigrade for periods varying from one to ten minutes, depending upon the species Chill ing has been used with wheat[34] and rice [20] with temperatures around freezing Use of hot or cold water is a simple procedure since a Thermos flask may be filled with water at the desired tempera ture and taken into the field, and the flowers may be immersed in the water for the necessary period of time Hot water is used to open the flowers of rice, after which the anthers are removed with forceps Self pollen of lucerne has been killed by immersing the flower in 57 per cent ethyl alcohol for a period of ten minutes [24], [36]

3 *Pollination without emasculation* Self incompat ible lines may be found in tobacco, potato, a few varieties of mustard, and many forage legumes In highly self sterile plants emasculation may be unnecessary for the production of hybrid plants in which case the breeder depends entirely upon the greater compatibility of cross pollen to ferti lize the ovule The method has been advocated also for self pollinated crops[13] if marker genes are present to identify the selfs but this procedure appears to be of doubtful merit if accurate results are desired

4 *Male sterility* Genetic male sterility, condi tioned by the presence of recessive genes has been used to eliminate the emasculation process in barley

crossing [38] Cytoplasmic male sterility is used to facilitate the commercial production of hybrid seed in onions, maize, sorghum, bajra, wheat, sugar beets and other crops

The exact procedure for emasculation must be learned for the particular species with which one is working It is often necessary to remove various bracts, petals, or sepals before emasculation, and plants differ in the degree of shock that this imposes on the flower In wheat, barley, and rice the bracts may be cut back severely without undue effect, but the same treatment in oats would virtually prohibit any seed setting The timing of the emasculation is important If the operation is delayed too long, the anthers may burst and spill pollen as they are being removed On the other hand, emasculation at too early a stage, while the flower is immature and tender, will result in unnecessary mutilation of the pistil After emasculation, the flowers are covered with parchment or glassine envelopes, or kraft paper bags, to protect them from stray pollen

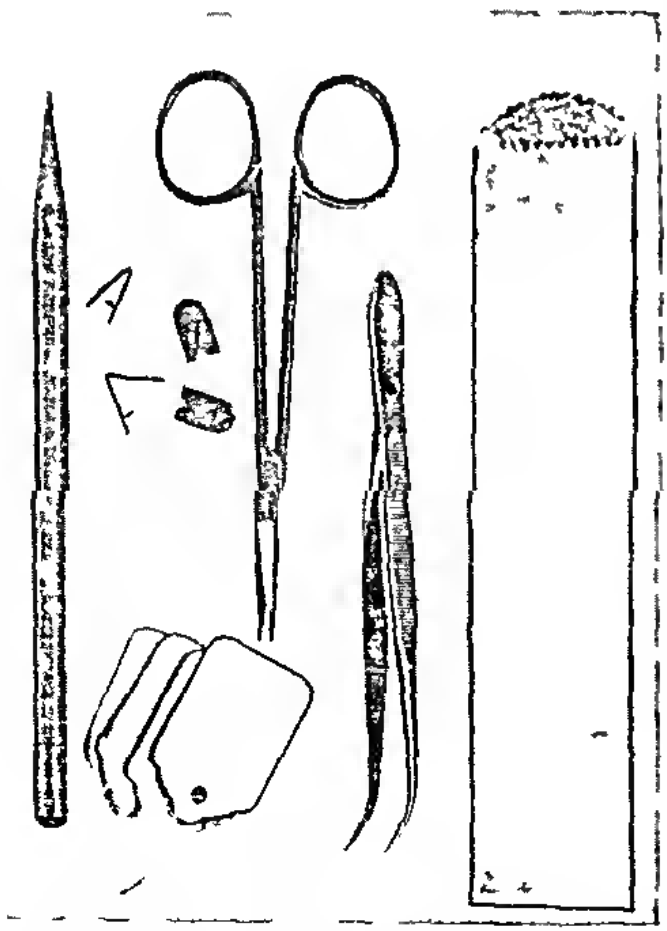


Fig 5 5 Equipment commonly used in emasculating and crossing rice, wheat, and barley Either curved- or straight pointed tweezers may be used The head bags may be made of glassine or butter paper

Pollination Practices. Pollination must be made during the period that the stigma is receptive This may be indicated by the opening of the flower and the full development of the stigma [29] In some species, such as rice, soybeans, cotton, and tobacco, pollinations may be made on the same day that the flower is emasculated In many species, pollinations are usually delayed from one to three days after emasculation (Fig 5 3) Pollination is carried out by collecting ripe anthers and emptying the pollen from a dehiscing anther upon the stigma The anthers are handled with fine-pointed forceps, or the anthers may be crushed and the pollen dusted over or rubbed on the stigmas by means of forceps, toothpicks, small pieces of cardboard, or camel's-hair brushes In some cases the shedding panicle can be shaken over the clipped and emasculated florets It is essential that the pollen be mature and fresh Pollen collected from green anthers, several hours before they would dehisce naturally, will usually give unsatisfactory results The length of time that pollen remains viable varies greatly At high temperatures, the pollen of wheat or oats may not remain viable for more than a few minutes, and that of maize may be killed in a few hours With proper storage pollens of maize and sugar cane have been kept viable for several days, and that of birdsfoot trefoil for several months Pollen of the date palm has been used successfully after ten years To retain viability, pollen should be stored at a cool temperature and in a high relative humidity

Flowering of most crop plants occurs in the morning, so pollen is collected and pollinations made at that time Oats flower throughout the day, and success is usually obtained by making the pollinations in late afternoon Pollinations are most successful when made on bright, warm days, little is accomplished on cool, cloudy days

Insects may be used to cross pollinate certain crops like mustard and lucerne [39] The parent varieties are enclosed in an insectproof cage Bees or other insects, which have been cleansed first of pollen, are introduced into the cage A high degree of incompatibility is usually depended upon to prevent self or sib pollination

Practices to Control Flowering. Many crosses

are made in the glasshouse during the winter months so that this tedious and time-consuming operation will not fall at the period of optimum note-taking in the field By making crosses of annual summer growing crops during the winter months, an extra generation is usually gained over the time required when the crosses are made in the field Also, contaminations from wind-blown pollen may be reduced by glasshouse pollinations Glasshouse pollination often requires use of various procedures so that plants with different maturities will flower together Procedures used include *temperature control*, *regulation of day length*, and *vernalization* Flowering may be speeded up by growing plants in higher temperatures, or flowering may be delayed by reducing the temperatures in which the plants grow Long day plants may be brought into flowering during the winter months by increasing the day length with artificial lights or by interrupting the period of darkness with a short period of light about midnight The same techniques may be used to prevent certain short-day plants from flowering prematurely Crops with a winter growth habit, such as winter wheat, usually need to be vernalized to obtain flowering inside the glasshouse Vernalization of winter grains may be accomplished by keeping germinated seeds between moist blotters at a temperature of 1 to 3 degrees centigrade for a period of four to six weeks Another practice is to plant the winter varieties outside, and then transplant to the glasshouse after the plants have been exposed to sufficient cold to break the winter growth habit Vernalization is not a problem with varieties commonly grown in south and southeast Asia If the two parents differ in time of flowering, successive dates of planting for one or both parents may be made in order that simultaneous flowering may be obtained

Use of Embryo Culture with Wide Crosses. After crossing in wide species crosses, it may be exceedingly difficult to obtain viable F_1 seed that will develop into a plant In some cases it is possible by excising the embryo from the remainder of the seed and by culturing it aseptically on an artificial medium to obtain its germination and development into a hybrid plant [50] Embryo culture has been used as a tool to obtain hybrid plants in difficult crosses with barley, sweetclover, fruit trees, forest trees, and various vegetable crop plants Hybrid embryos of a cross between low-coumarin white sweetclover, *Melilotus alba*, and common yellow sweetclover, *M officinalis*, were reared by the use of embryo culture (Fig 5 6) Hybrid plants from this cross reached maturity and bore seeds

TECHNIQUES IN CONDUCTING FIELD TRIALS

The proper conduct of field trials is of major interest to the plant breeder In his search for a new variety the breeder usually finds it necessary to grow a very large assortment of experimental strains Most of the strains will be inferior in some respects If their undesirable features can be recognized, they may immediately be eliminated from further consideration In ordinary practice the procedure is first to grow large numbers of new strains, which have a limited seed supply, in small observation plots where the breeder evaluates their maturity, height, lodging, disease resistanee, and other characteristics, including over all vigour From these visual observations the breeder selects what appears to him to be the superior strains The superior strains are then grown in replicated field trials to determine more accurately their potential performance, including yield, in comparison with standard commercial varieties Since replicated field trials are more expensive to conduct, fewer strains are tested in them in comparison with the very large numbers of strains that may be grown in the preliminary observation nurseries

Even when outstanding experimental strains are encountered their yield superiority over the best commercial varieties will generally be small For this reason the breeder strives to measure small differences in the potential yielding ability of strains, a condition requiring that the performance trials be conducted with precision and accuracy if they are to measure correctly differences in the performance of the breeding materials The need to measure small yield differences accurately is most important in advanced trials in which only elite strains are being tested By this time the breeder will have already eliminated the strains that were found grossly inferior by the observation nurseries and in preliminary yield trials

It is not within the scope of this text to present a comprehensive discussion on the conduct of yield trials This information is contained in textbooks dealing with field plot experimentation and the statistical analysis of data The student who expects

5 6A 5 6B 5 6C

F g 5 6 Embryo culture used to rear embryos of species hybr ds in sweetclover A Embryos reared on agar Starting at the top the embryos are shown at 7 8 9 10 11 12 and 14 days after pollinat on E Vials in which hybr d embryos from a cross between low coumarin white and common yellow sweetclover were reared in diffused light and controlled tempera tures unt l leaves and roots were well established The embryos are lying on or just below the surface of the agar C Hybrid plant of a sweetclover species cross that was grown to maturity from an embryo reared on agar Flowers on this plant were selfed or backcrossed to the parents and bore seed

to continue in the field of plant breeding will need to become conversant with their content Only a brief summary of the principles of field experi mentation is presented here for the guidance of those students whose training may be terminated before they reach a formal presentation of this subject yet who may later find it necessary to conduct simple yield or demonstration plots as many cultivators extension officers or agricultural teachers are called upon to do Also familiarity with the principles of variety testing may be useful to students who some day may need to evaluate and interpret the results of performance trials.

Nursery vs Field Plots *Nursery plots* are small, single or multiple row plots in which varieties of field crops are grown for observation or yield trials The size of the plots will vary with the crop the amount of seed available and the nature of the observations which the breeder expects to make The nursery plot is used when (*a*) the seed supply of the strain is limited and when (*b*) a large number of strains is to be tested

The seed supply of most experimental strains is limited in the early breeding stages and many thousand experimental strains are tested by the breeder so nursery plots are used for preliminary evaluations of most breeding materials Since nursery plots are small they are planted and har vested by hand or with special planters and har vesters constructed for nursery use

Field plots are of such size and shape that they may be planted and cultivated with standard farm implements Usually field plots vary from 1/10 to 1/100 acre in size Field plots more closely simulate actual field conditions than do nursery plots They are valuable as observation plots because their size makes it easy for the breeder to make visual observations of the performance of a variety They

are useful for making preliminary seed increases Field plots require more seed and are more expensive for testing a given number of varieties than are nursery plots In general, field plots are used only for testing a few elite experimental strains and standard varieties, after the superiority of a strain or variety has been demonstrated in nursery plots

Principles in Plot Technique The purpose in making variety performance trials is to measure *comparative yields, maturity, height lodging disease resistance* and other characteristics of varieties and experimental strains of a particular crop It is essential that an adapted commercial variety be included as a check to which the performance of experimental strains and new varieties may be related A certain amount of error is present in the performance of varieties in any field experiment The error may arise from chance fluctuations in the yield of the strains due to unavoidable situations, or it may arise from faulty and careless technique in the conduct of the experiment If the error is large, the experimenter may learn very little from the experiment, or he may be misled and unable correctly to evaluate varieties from the data obtained In order to have accurate and trustworthy results, the experimenter must follow careful and proven procedures that are uniformly carried out with all the strains included in the test, and he must eliminate personal bias in recording notes and in interpreting the data As with so many undertakings, *good plot technique is simply the exercise of sound judgment, combined with a few rules of procedure that have been learned from long experience*

A SOIL VARIABILITY The variability in the soil is one of the most universal sources of error in field plot trials Even in small contiguous areas, the soil may vary to such an extent in fertility, drainage, or texture that plants of similar heredity growing within a few feet of each other will perform differently Previous soil treatments often leave residual effects that affect the growth of the succeeding crop For these reasons soil areas used for performance trials should be carefully selected, with consideration given to such factors as topography, drainage, fertility, previous treatments, and uniformity It is often helpful to observe the uniformity of the preceding crop before selecting the exact area to be used for a performance trial Generally, plots that are long and narrow will most effectively sample the soil variations, if the long dimension of the plot is in the direction of the gradient in soil fertility

B COMPETITION AND BORDER EFFECT Crop plants in adjacent rows compete for the soil moisture and plant nutrients in the space between them A vigorously growing variety may adversely affect the performance of a variety in an adjacent row, especially if moisture or nutrients are limited Tall growing varieties may shade shorter varieties in adjacent rows The performance of varieties growing in adjacent rows may also be affected by differences in maturity, lodging, or type of growth To reduce the error resulting from competition between varieties, it is a common practice to plant nursery yield tests in three row plots and harvest only the center row, or to plant four row plots and harvest the two center rows Competition between varieties may be reduced by grouping together varieties that are similar in maturity and growth characteristics Plants of the same variety within a single row compete among themselves For accurate yield results it is important to have uniform stands of all varieties in a test

Series of nursery and field plots are usually grown in small blocks separated by blank spaces, or alleys Plants growing at the end of the rows or in outside rows are usually more vigorous and productive than plants within the row, since the border plants have less competition than the plants in the interior of the plot In small nursery plots, the *border effect* may affect greatly the yield of outside rows To eliminate border effect, it is a common practice to plant along the sides of the plots several rows of a standard variety which are discarded before harvest, and to cut back and discard the ends of the plots before harvest

C REPLICATION In the conduct of yield trials, the recorded yield of a plot is always subject to some error The true yield of an individual plot will be either larger or smaller than the recorded yield, depending upon the extent and the direction of the error If the error is due to chance, it may be expected that the yield of different individual plots of the same variety will fluctuate around the true yield If the yields of several plots of the same variety are averaged, the chance fluctuations will tend to offset each other For this reason, the mean yield of several plots of a variety is a better estimate of the true yielding ability of a variety than the yield of

a single plot The number of times a variety is repeated in an experiment is commonly referred to as the *number of replications* This may range from three to ten replications, depending upon the design of the experiment, the accuracy desired in the yield data, and the amount of land and seed available In most standard yield trials, either four or five replications are planted Replication is necessary to sample effectively the variations in soil fertility *Replication provides the means for estimating the magnitude of the error in any particular experiment* This fact will be appreciated by the student after he has completed courses in the statistical analysis of data More replications are commonly used for performance trials that are harvested for yields than those grown for observation only

D LOCATION AND SEASONAL VARIATION Varieties perform differently in different locations and in different seasons Consider the example of a variety test with maize, on a fertile loam soil with adequate soil moisture throughout the growing season, in which the early varieties were outyielded by the late varieties because the latter had larger plants and ears In another location where moisture became limiting toward the end of the season, the early varieties yielded the most grain because moisture ran out before the late varieties were fully developed Or consider the yield of two adapted varieties of wheat, one resistant to black rust and the other susceptible In a season without rust damage, the susceptible variety might outyield the resistant But in a season with severe rust damage, the resistant variety would surely outyield the susceptible

Variations in performance of varieties at two locations may be due to differences in the soil or to differences in the climate Variety tests are generally conducted at several locations within a state or region to determine the response of the varieties to varied soil and climatic conditions Uniformity nurseries grown over a wide geographic area are useful for determining the range of adaptation of individual strains and varieties over large regions Since varieties may respond differently in different seasons, they are tested over a period of several years to determine the consistency of their performance Usually three to five years of testing at several locations in a particular region are considered necessary before a variety can be safely recommended there.

Plot Design. Variety tests are generally conducted to measure difference in variety performance only The design of the experiment may be simpler than the design used for complex field experiments set up to measure the interaction of two or three factors The specific design that may be used in a variety test will depend upon the particular crop, the number of varieties to be tested, and the precision desired in the results Three simple plot designs that may be used are illustrated here The randomized block and the Latin square are perhaps the most widely used and desirable experimental designs for variety testing

A SYSTEMATIC ARRANGEMENT In a systematic arrangement the varieties are arranged in the same order in every replication (Fig 5 7A) The systematic arrangement offers a simple arrangement in which varieties of similar breeding or maturity can be grouped to facilitate note-taking or harvesting The principal objections to this arrangement are

1 Errors from competition may be magnified since the same varieties always fall next to each other

2 *There is no way to analyze the data to obtain a valid estimate of the amount of error*

B RANDOMIZED BLOCKS In a randomized block design, all varieties appear in each replication of the experiment and are arranged in a random order within the replication (Fig 5 7B) Replications may be placed end to end or opposite each other, although it is generally preferable that the total area covered by the experiment be as nearly square in shape as possible The randomized-block experiment is simple and eliminates the principal objections to the systematic arrangement For accurate results the randomized block is limited to tests with a small number of varieties

C LATIN SQUARES In the Latin square plot design, the number of replications equals the number of varieties Each variety appears once in each of the replications (rows) and in each column (Fig 5 7C) The number of varieties is limited in the Latin square experimental design since there must be the same number of replications as varieties This type of experiment samples soil variability more accurately because the varieties are placed in both rows and columns It is a simple design to analyze from a statistical standpoint

If large numbers of varieties are to be tested in a

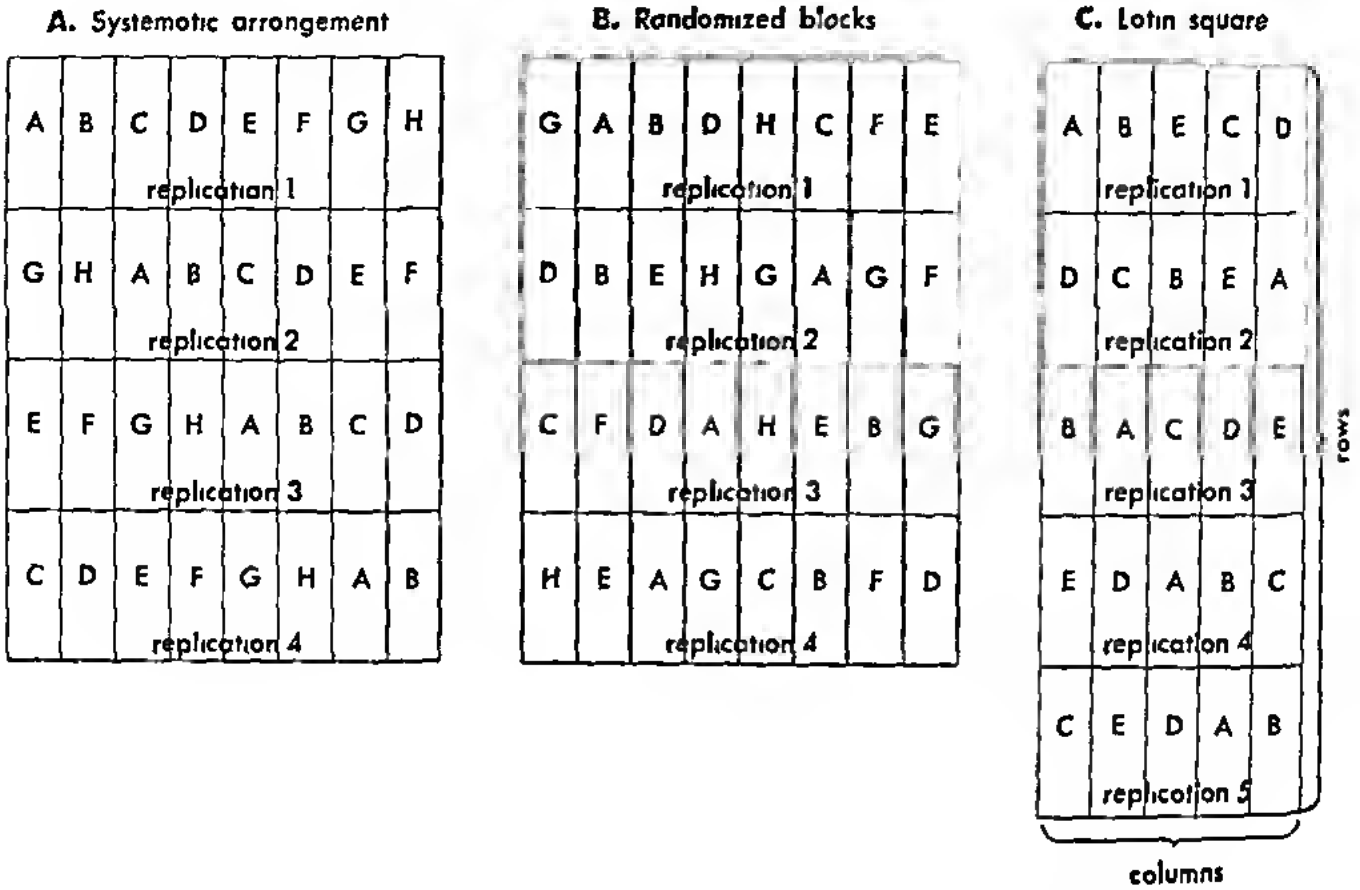


Fig 5 7 Field plot designs A Systematic arrangement B Randomized blocks C Latin square

yield test, other plot designs which are more complicated in layout and analysis will need to be used *Without a proper plot layout it is impossible to calculate a valid estimate of error* Regardless of the plot design, accuracy and careful attention to details in planting, harvesting threshing and weighing are required to obtain accurate results *No plot design or method of analyzing data will compensate for careless and sloppy work*

Difference Necessary for Significance. It is a common practice in publishing reports of yield trials to list the difference necessary for significance between varieties The value is obtained by first subjecting the yield data to a statistical analysis known as an *analysis of variance* From the analysis of variance test the breeder learns whether the mean yields of the varieties are significantly different as a group, but he does not learn whether a particular variety differs from another or from a check variety within the group To obtain this information additional statistical tests are made One, called *least significant difference* (or L S D) works in this manner Suppose variety A yields 32 quintals, variety B yields 26 quintals, the check variety with which they are being compared yields 28 quintals and the L S D of the experiment is 3 5 quintals By adding and substracting 3 5 from the yield of the check, a range between 24 5 and 31 5 quintals is obtained over which the check variety may vary In this experiment variety A falls outside of the range, so is recognized as significantly different from the check, but variety B is not adjudged to be different from the check for it falls within the range To compare a group of varieties with each other, different tests are used In each case the reliability of the comparisons are generally based on odds of 19 1 Details of procedures for calculating analysis of variance and "significant differences" are not described here, but can be found in standard statistics textbooks

MATURITY COMPARISONS

Comparative maturity is one of the most common observations made by the breeder on strains and varieties of crop plants The range in maturity that is desired in a specific crop will depend upon

where the crop is being grown, the use that will be made of the crop, the crop rotation practice, and the need for escaping disease, insects, or other natural hazards Maturity is influenced by the inheritance of the plant and the environment Environmental factors that may affect the time of maturity are response to day length, temperature, altitude, soil type, seasonal distribution of moisture, and others The environmental influence on maturity must be considered in comparing the inherent maturity differences in varieties

The comparative maturity of varieties of a crop is expressed in various ways, some of the more common being date of flowering, date of heading, date silked (maize), or date ripe With crops like rice, wheat, barley and oats, date of heading is considered a more accurate index to maturity than date ripe, since it is influenced less by abnormal temperatures, deficiencies in soil moisture which cause premature ripening, or other environmental factors Other indexes used with these crops are date of emergence of awn or spikelet from the boot and date 75 percent of the plants have flowered Sometimes the number of days earlier or later in maturity than some standard variety is used as an index to comparative maturity In maize, date of silking is a common index of maturity, although percent of moisture at the time of harvest also gives a measure of relative maturity Earliness in cotton is determined by the time of first flowering, the length of the boll forming period, and the time required for the bolls to ripen The percentage of lint at first harvest is a common means of comparing earliness of maturity in cotton

RESISTANCE TO LODGING AND SHATTERING

Lodging is the bending or breaking over of the crop before harvest Lodging causes large annual losses in rice, wheat, maize, millet, and other crops Although lodging depends on straw or culm strength and plant height, yet the amount of lodging varies from year to year, and is influenced by the rain and windstorms prior to harvest, and by damage from disease, insects, rate of nitrogen fertilization and other causes Unlike the measurement of yield, which may be recorded as a fairly exact numerical quantity, the *evaluation of lodging resistance is almost entirely a visual appraisal It is obtained by comparing the relative amounts of bending or breaking over of varieties growing in adjacent nursery or field plots* Obviously, it is necessary that all varieties be grown under as nearly identical conditions as possible and that some standard variety be included as a check with which experimental strains or new varieties may be compared In seasons in which the crop stands well, without natural lodging the observations of the breeder may be of little consequence The best observations are made in seasons with severe lodging A heavy rain or windstorm before harvest, although it may cause great loss to the cultivator, may be welcomed by the breeder if it permits him to select the strains with superior lodging resistance Lodging of an intensity to permit accurate differentiation of varieties does not occur regularly Hence, the breeder grows varieties in tests at several locations and over a period of seasons in order to make lodging observations under widely different environmental conditions Lodging may be intensified by liberal fertilizer applications, especially those fertilizers high in nitrogen Sometimes special nurseries are grown in which the varieties are permitted to stand for long periods after they are ripe in order to observe lodging under those conditions

Lodging observations are recorded in different ways by different breeders A common method is to record lodging on a percentage basis In this system, zero lodging would indicate that all plants are standing erect One hundred percent lodging would indicate that all plants are lodged Lodging notes are also recorded on a scale of 1 (plants erect) to 5 (heavily lodged), or a scale of 1 to 10 In maize, lodging is generally expressed as percent of plants with root lodging (leaning more than 30 degrees from the vertical) and percent of plants with stalk lodging (stalk broken below the ear) (Fig 5 8)

Various laboratory methods have been devised to measure lodging by exacting mechanical procedures, or to measure the characteristics of plants that may be associated with lodging Breaking strength of straw[37 40] and weight per unit length of straw[3] have been used as an index to lodging resistance in cereals like wheat and oats The number of coronal roots was found to be related to the lodging resistance in oats[15] Lodging resistance in rice and oats has also been estimated by the amount of bending caused by a chain hung from the base of the panicle[12 18] In maize, lodging resistance has been measured by the force necessary

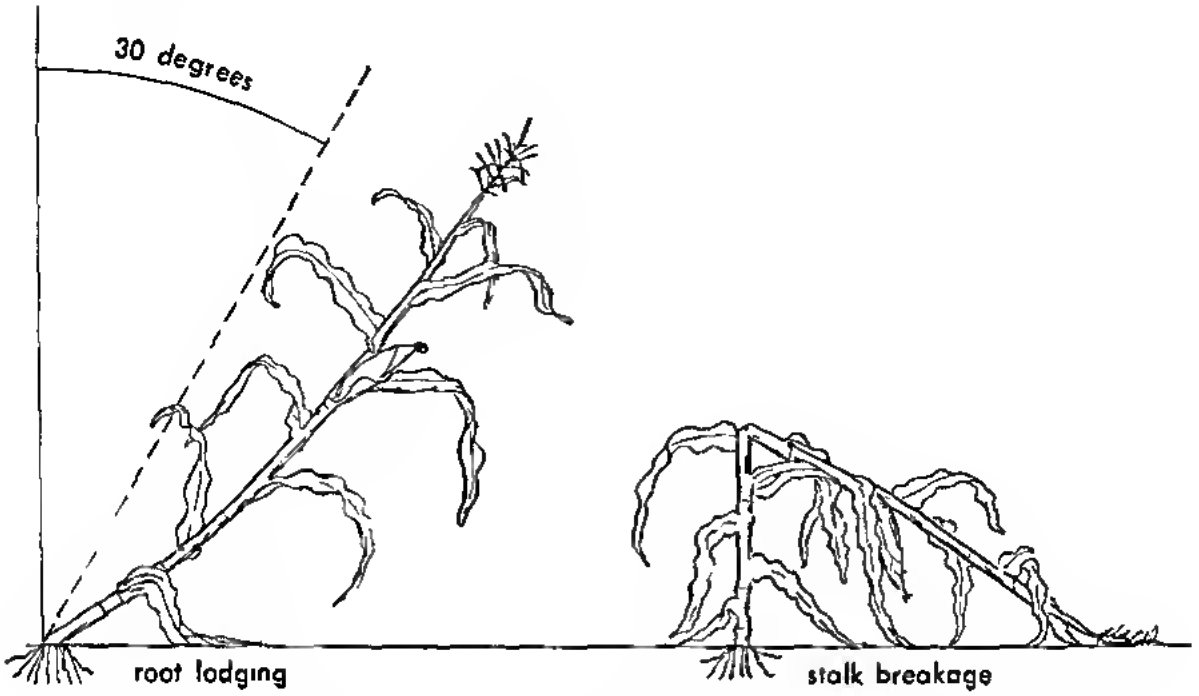


Fig 5 8 Types of lodging in maize Lodging in maize is generally expressed as *root lodging* if the stalk leans more than 30 degrees from the vertical or *stalk breakage*, if the stalk is broken below the ear

to pull inbreds or hybrids out of the ground [14]

Shattering refers to seed that falls out and is lost before harvest or during the harvesting operation Resistance to shattering is important to prevent loss in rice, wheat, linseed, sesame, and some other crops Visual estimates of loss are commonly made o compare the resistance of varieties to shattering Numerous laboratory methods have been studied to find a mechanical means of measuring the resistance to shattering [15] The only satisfactory methods studied involved measurements of the strength of the glume attachment and a machine to beat out the grain with a paddle

HEAT AND DROUGHT RESISTANCE

Resistance to heat and drought,[25] [26] are important objectives in the breeding of many field crops Testing resistance of varieties to these adversities may be done in the field, the breeder depending upon unfavourable seasons to produce differential injury, or laboratory tests may be conducted which simulate the unfavourable effects of these adversities

Damage by heat and drought to wheat, maize, potato, sorghum, bajra, and other crops is common in many low rainfall areas Differences in the extent of injury have been noted in different varieties of these crops In most areas where breeding experiments are conducted, observations on heat and drought resistance cannot be made every year in the field, because differences in varieties do not occur regularly Also, it is generally impossible to separate the adverse effects of heat from the adverse effects of drought by field observations alone For this reason attempts have been made to measure resistance to these adversities in the laboratory by various means [2] Some of the most satisfactory results have been obtained by wilting tests in which plants are subjected to (*a*) high temperatures, (*b*) soil drought, or (*c*) atmospheric drought Recovery from these treatments is used as a measure of the comparative heat or drought resistance

Varieties of oats were found to differ widely in their ability to resist heat when plants in the five leaf stage were subjected to temperatures of 48 5 to 52 degrees Centigrade for a period of 45 minutes [19] A similar method was used to compare the heat resistance of different strains of maize [16] The effect of soil drought on varieties of wheat was studied by withholding water from plants in the tillering stage until they wilted The plants were held in the wilted condition for three days, after which water was added to bring the soil to optimum moisture [1]

Varieties were also tested for resistance to atmospheric drought by placing them in a chamber and forcing air heated to a temperature of 100 degrees Fahrenheit, and with a humidity of 13 to 17 percent, over them at a velocity approximating six miles per hour[1] In studies to differentiate varietal resistance to heat or drought it is important that all plants be tested at a similar stage of development

TECHNIQUES IN BREEDING FOR DISEASE RESISTANCE

The possible control of disease through host resistance is an important biological principle that is well established Plant breeders have been consciously selecting varieties for disease resistance since before 1900, but the selective forces of nature have been operating since the beginnings of plant life Breeding for disease resistance involves a few well known principles and some commonly used procedures These may be summarized as follows

1 Resistance to a specific disease is not acquired or created Genes for resistance must first be found in some variety or closely related species

2 After resistance genes are known, they may be transferred to an adapted variety by standard hybridization procedures

3 Many of the disease inciting organisms are composed of various specialized biological forms, known as *biotypes* or *physiological races*, which differ in their pathogenicity on different varieties of the same crop Varietal resistance is thus an expression of both the genotype of the host and the genotype of the parasite and is conditioned by predisposing factors in the environment

4 The mode of inheritance of resistance to many specific diseases or biotypes of diseases appears to be rather simple with only one or two major genes involved Resistance may be either dominant or recessive, although the dominant reaction is the more common Resistance in other varieties, or to other diseases, is more complex with numerous genes affecting the host parasite relationship

5 In breeding for resistance, exposure to the disease, either in natural or artificially induced epiphytotics, is necessary to distinguish between the resistant and the susceptible plants

6 Progeny tests of resistance plants are made to verify the inherent nature of the resistance and to ensure that uninfected plants have not merely escaped infection

The basic problem in the technique of breeding for disease resistance is that of providing a disease environment in which to grow the crop so that the resistant plants may be distinguished from the susceptible Since natural disease epidemics do not occur in the field every year, it is desirable for the breeder to be able to establish disease epiphytotics by artificial means, either in the field or in the glasshouse, so that he is not entirely dependent upon the vagaries of nature to provide him with an adequate disease environment Close cooperation between the plant pathologist and the plant breeder is desirable in order that (*a*) the plant materials being tested will be exposed to the proper biotype or range of biotypes of the organism, (*b*) the intensity of the disease incited will be adequate to differentiate between the plants or strains in the test, (*c*) the resultant strains will be selected both from the standpoint of disease resistance and agronomic characters that will adapt them for agricultural use

In the final selection of varieties for the cultivator to grow it is often necessary to compromise between superior disease resistance and superior adaptation when both characteristics are not found in the desired intensity in the same variety

With any inoculation technique, it is important that all varieties tested be treated in as uniform manner as possible Both resistant and susceptible varieties with well defined reactions to the biotype of the organism being used should be included as checks Artificial inoculations should closely simulate natural infections Detailed descriptions of the many artificial inoculation techniques used to initiate epiphytotics of specific diseases cannot be described in detail Here, discussion will be limited to a general review of the nature of the procedures used with various types of diseases, and references cited at the end of the chapter may be used for further reading if additional information is desired

Inoculation Techniques for Soil-Borne Diseases. Certain diseases are incited by soil borne pathogens that enter the host plant through the roots or other underground parts These include such important and widespread diseases as cotton wilt, rhizoctonia rot of cotton, crown and root rots of barley, root and seedling rots of maize, wilt of pigeonpea, root rot of jute and flax wilt Field tests to determine varietal resistance to these diseases may be conducted by growing the varieties

in soils in which the disease-inciting pathogen is prevalent The intensity of the disease may be increased, in some cases, by collecting soil from other diseased fields and scattering it over the test plot, or by inoculating the soil with cultures of the causal organism grown on sterile grain or on other types of nutrient media The same soil area is then used again in succeeding years Glasshouse tests may be made to determine resistance by growing the varieties in containers filled with infested soil (Fig 5 9) [27] The infested soil may have been obtained from diseased fields or by mixing cultures of the causal organism with sterilized soil Glasshouse tests often differentiate varieties better than field tests because temperatures favourable for the growth and development of the disease inciting organism may be maintained Various modifications of these testing procedures have been developed In the cold test for maize, seeds of inbreds or hybrids are germinated in contact with soil from disease-infested fields [17] The temperature is maintained below the optimum for germination of the maize, but near the optimum for the development of the soil-infecting organism This simulates early spring planting in cold, wet soils A method of mass testing of seed has been reported in which germinating seed is sprayed with a suspension of the disease inciting organism [33] Normal, healthy seedlings are transplanted to soil and grown to maturity, and diseased seedlings are discarded Varieties may be rated by comparing percentages of normal and diseased plants

Inoculation Techniques for Foliage Diseases. Many disease-inciting organisms infect the plant by entering through natural openings, such as stomata or lenticels, or through wounds inflicted during cultivation or harvesting by insects or other means These include a large variety of diseases such as blast of rice, rusts of wheat and barley, rust of sorghum, brown leaf spot of sugarcane, early blight of potato, anthracnose of cotton, smut of maize and rust of linseed Inoculation techniques for these diseases may range from dusting dry spores on the foliage to spraying the plant with a suspension of spores and mycelium of the disease inciting organisms (Figs 5 10, 5 11) Several procedures may be used to obtain better infections Some of these are

1 Maintaining a temperature around the host plant during the infection period that will be optimum for growth of the disease-inciting organism

Fig 5 9 Testing sorghum varieties for resistance to milo disease by growing them in disease infested soil The healthy, resistant varieties may be easily identified from the diseased varieties

Fig 5 10 Collecting rust spores from an infected plant of wheat by suction The rust spores are used to produce new infections on healthy plants By this means the comparative rust resistance of varieties to specific cultures of the rust organism is learned

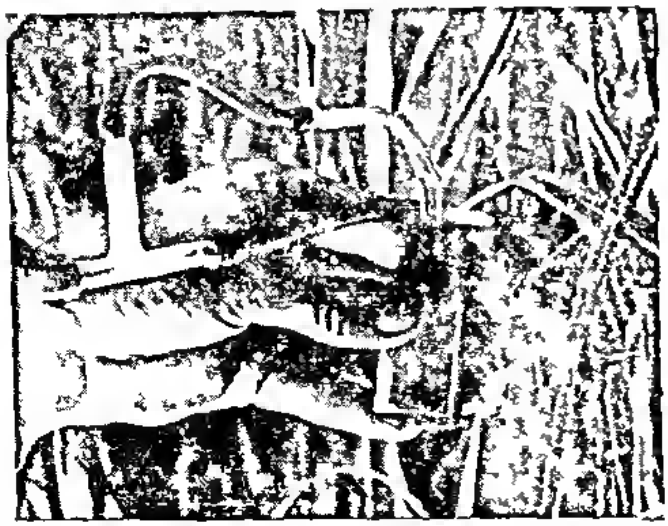


Fig 5 11 Dusting rust spores on wheat plants in an incubation chamber in the glasshouse The plants are first sprayed with water to ensure good dispersal of the rust spores The wheat plants are kept in a warm humid atmosphere to permit the rust disease to develop

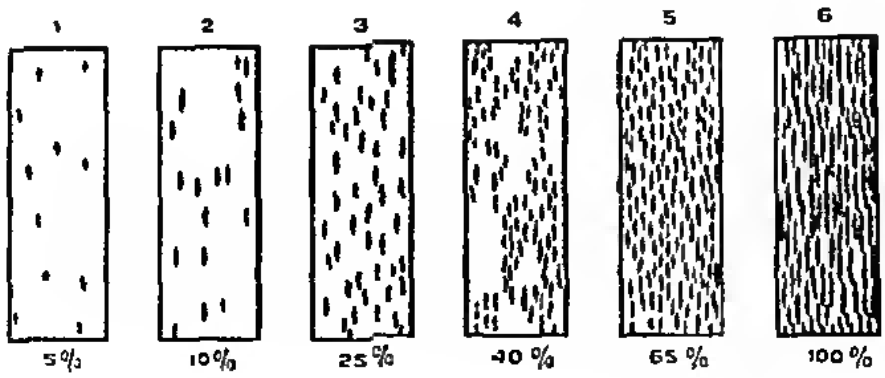
2 Controlling the humidity during the infection period by surrounding the host plant with a moist chamber in which the atmosphere can be maintained at or near saturation (Fig 5 11)

3 Spraying the host plant with a suspension of the disease inciting organism during the periods of the day when the stomata are open widest so as to have the germinating spores or infection processes in close proximity to the open stomata [11]

4 Reducing the surface tension of the suspension to permit an even spread of the inoculum by adding a small amount of a mild detergent or by rubbing the waxy bloom off the leaves before dusting them with dry spores

Temperature and humidity can be controlled with more accuracy in the glasshouse than in the field this makes glasshouse inoculations preferable to field inoculations if adequate glasshouse facilities are available Sometimes tents are erected over segments of field plots and plants under the tents are sprayed regularly with a fine mist to maintain a high relative humidity around the plant Application of bacterial inoculum with a power sprayer or hypodermic syringe may force some of the inoculum into the open stomata or cause water soaking of the leaves to aid entry of bacteria When testing varieties for rust resistance it is a common practice to plant a susceptible variety in adjacent areas to act as a rust spreader The susceptible variety is inoculated by using a hypodermic needle to inject a spore suspension into the whorl of the developing plant or by using a fine miscible oil spray containing the inoculum Infection pustules develop and spores are spread to adjacent plants and varieties by natural means The intensity of the infection is determined by estimating the area of the plant covered by the disease (Fig 5 12) by rating plants for disease damage and by other means

Inoculation Techniques for Floral Infecting Diseases Certain diseases such as the floral infecting loose smuts of wheat and barley are initiated by spores from smutted heads entering open blossoms of normal heads where they germinate and infect the developing kernel Inoculation techniques used with these diseases consist of introducing ripened spores into the flower at the time of anthesis [8 9] Dry spores may be introduced with a pair of forceps or a hypodermic needle or a spore suspension may be made and injected into the



5 12A

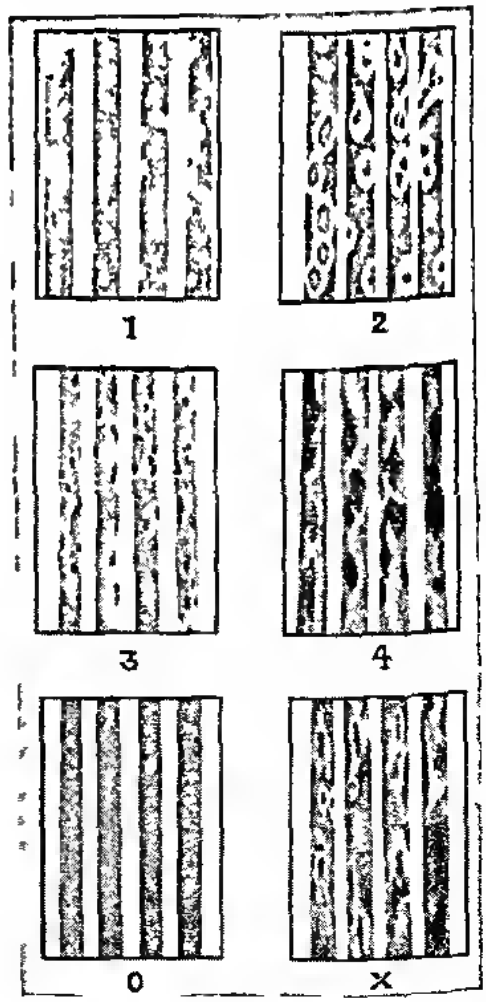
Fig 5 12 Estimating severity and type of rust infections. A Scale for estimating percentage of rust infections on the leaf or stem The shaded areas represent rust and the figures represent the approximate rust percentage The diagram on the right (No 6) is arbitrarily selected as 100 per cent although only 37 per cent of the surface is covered with rust, because this is the maximum infection that would normally be encountered in the field The rust percentages of the other diagrams Nos 1 to 5 are computed in relation to the coverage of No 6 B Infection types produced on different varieties of wheat by physiologic races of wheat stem rust (*Puccinia graminis tritici*) The infection types are 0 (immune), 1 (highly resistant) 2 (resistant) 3 (susceptible) 4 (completely susceptible), and X (mesothetic, in which resistant and susceptible types occur on the same plant)

flower with a hypodermic needle, by means of vacuum or pressure Seeds produced in the inoculated flowers are harvested and planted, and the percentages of smutted heads or plants are determined the following season

Inoculation Techniques for Seed-Borne Diseases. Some smut diseases are seed borne and inoculation techniques used with these diseases consist of applying the spores to the seed before planting With bunt of wheat and covered smut of sorghum, the spores are dusted on the dry seed Oats may be dehulled and dusted with spores, but this procedure will usually reduce germination A more common inoculation technique with oats smut or covered smut of barley is to soak the seed in a spore suspension under vacuum The vacuum withdraws the air from under the hulls and permits the spore suspension to penetrate under the hull when the vacuum is released Percentages of infected heads or infected plants are commonly recorded

Many other disease inciting organisms are both seed borne and soil borne These include such diseases as cotton wilt and the *Gibberella* and *Diplodia* organisms which incite root, stalk and ear rots of maize Inoculations with these organisms are generally made through the soil

Inoculation Techniques for Insect Transmitted Diseases. Some diseases are insect-transmitted Many of the virus diseases are transmitted by this means Artificial inoculation techniques



5 12B

with these diseases may utilize the following procedures

1 *Insect transmission* Insects commonly aphids or leafhoppers which have fed on infected plants are collected and transferred to healthy plants Plants are generally grown in insect tight cages to prevent natural movement and infection from insects (Fig 5 13)

2 *Mechanical transfer* Diseased plant tissue is macerated and the extracted juices rubbed over the leaves of healthy plants with sufficient force to cause slight mechanical injury A fine abrasive such as carborundum powder may be dusted over the leaves first, or mixed with the juices, to aid in obtaining injury

TECHNIQUES IN BREEDING FOR INSECT RESISTANCE

The principles and techniques used in breeding for insect resistance do not differ in substance from those used in breeding for disease resistance It is necessary that (*a*) sources of resistance genes be located (*b*) genes for resistance be transferred into adapted varieties by hybridization procedures and (*c*) varieties be exposed to insect populations so that the resistant strains may be distinguished from the susceptible strains

Biotypes, or races in certain insects have been identified which are more or less comparable to biotypes or races in diseases The breeder should be sure that he is exposing the varieties being tested to biotypes of the insect comparable to those that will be encountered in the field when the variety is distributed to the cultivators Cooperation between the entomologist and the plant breeder is essential in the development of an insect resistant variety, just as cooperation between the plant pathologist and the breeder is essential in the development of a disease resistant variety Insect damage is often related to the stage of growth and development of the plant and varieties under test should be uniform in maturity if inherent resistance is to be accurately measured

Techniques for determining resistance may be of two types

I *Natural insect populations* may be maintained in the field by cultural practices that favour propagation of the insect species The technique is used in the U S A in breeding for resistance to the Hessian fly by planting wheat during periods favourable for infestation in the same area every year The resistance of new varieties and strains planted in the infested area is determined by comparing their infestation with that of resistant and susceptible check varieties

2 *Artificially reared insect populations* may be transferred to plants in the field or in the glass house [6 7 28] Plants being tested are often placed in insect tight cages to keep the insect pests in contact

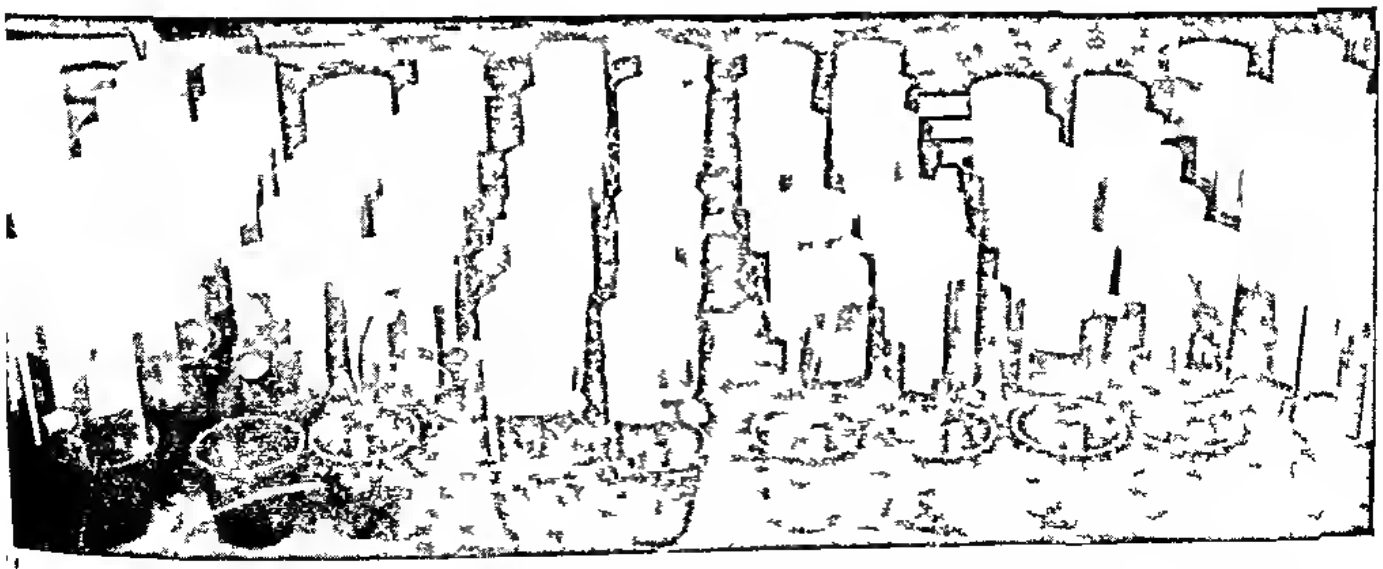


Fig 5 13 Rice varieties are screened for resistance to tungro a virus disease by caging them with leafhoppers which have previously fed on diseased plants

with the plants and to prevent infestation from other insects by natural means

MEASURING QUALITY

Techniques used to measure quality of field crops are determined by the particular crop that is under consideration and the use for which it is being grown The quality characteristics of wheat required for baking bread is quite different and much more exacting than those required for making chapatis The milling and cooking qualities of coarse rice differ from those of fine grained rice Spinning qualities of native short staple cottons differ from those of the long staple upland varieties *Measuring the quality characteristics of* a variety often is very complex The measurement of wheat quality requires a long series of testing procedures each of which evaluates a different component of wheat milling or baking quality These include such diverse characteristics as grain weight, protein and ash content of the grain and the flour, percent of bran removed in milling and yield of flour, water absorption and mixing time of the dough, loaf volume of the bread, and many other measurements Measurement of fibre and spinning qualities in cotton also involve complex testing procedures

The need for such detailed information about quality characteristics of varieties of crops which enter into commercial utilization increases as the procedures used by the baker, the spinner or the oil processor become more highly mechanized for then it is no longer possible to manipulate the mechanical processing at *will as is done with hand* processing With mechanization uniform raw products are needed for manufacture and marketing of uniform and acceptable finished products This is particularly the case with products like jute, tobacco and tea, which are important export crops from all of the south and southeast Asian countries Increased emphasis also needs to be placed on the nutritive value of food crops and to the absence of undesirable flavours or toxic substances in them

Some of the different quality tests which are more or less standard procedures in evaluating crop varieties, or which will become more important as technology of processing and manufacturing advances, include

Milling and baking properties of wheat for bread
Quality characteristics of wheat for chapatis
Milling and cooking qualities of rice
Oil and *protein content of groundnuts*
Oil content and iodine number in linseed
Fibre and spinning properties of cotton
Sugar content and purity of juice from sugarcane
Fibre quality of jute
Protein content and amino acid assays of maize
Oil content of rape and mustard
Nicotine and sugar content of tobacco

The nature and complexity of the quality characteristics of a variety should make it obvious that the plant breeder cannot carry through all the *quality testing procedures himself Most breeders* would have neither the time, nor the training, nor the laboratory facilities To measure fully quality components of most crops requires a specially equipped laboratory, staffed with chemists and other technically trained personnel, according to the specific crop being tested Various quality-testing laboratories of this type have been established in the major plant breeding research stations around the world

Through the facilities of the various testing laboratories, the breeder has the opportunity of obtaining fairly thorough tests of the quality of new varieties of many crops before they are released for commercial production For complete tests a large amount of seed or fibre may be required This limits the testing to advanced experimental strains which have already been proved superior in yield and other agronomic characteristics Most *breeders have need for simple quality testing* procedures that are inexpensive to perform and that can be used to screen large numbers of experimental strains, or even individual plants, before they have been advanced into yield tests For example, a simple test which measures kernel hardness of wheat kernels and which requires only a few grains of seed is used by wheat breeders to sort soft from hard strains in crosses between these two classes,[4] whereas a milling test with wheat requires several pounds of seed Other simple tests used for preliminary quality testing will be referred to in the chapters concerning specific crops Although the preliminary tests may not be as exacting as the more refined tests, they permit the breeder to select the strains with the best potential quality, which may then be subjected to more

thorough quality testing procedures after their superior agronomic characteristics have been demonstrated

KEEPING ACCURATE RECORDS

During the season a plant breeder will observe and evaluate thousands of strains (Figs 5 14 5 15) He will find that some of the strains have certain desirable features these he will choose to harvest so that he may observe their performance in another season Most of the strains he will consider unworthy of further attention and they will be left in the field to be harvested *en masse* and discarded after the desirable strains have been removed After the harvest the only records that show why certain strains were selected or rejected are the notes recorded in the field book Unless these are complete and accurate the breeder will be unable to evaluate the performance of the breeding materials he has grown and the operation of his breeding programme will be replete with duplication of work and inefficiency

Nearly every breeder has his own system of record keeping An efficient system of record keeping should possess the following requisites

1 *Completeness* The breeder should be able from his records to identify quickly the parentage of particular strains as well as their current performance The notes recorded on performance will vary with the crop but generally they should include such observations as height lodging relative earliness of maturity reaction to prevailing diseases or pests, and over all vigour If a yield test they will also include yield and quality evaluation of the grain fibre or forage Special identifying characteristics may be desirable to note even though they have little or no relation to performance

2 *Accuracy* Accuracy is necessary both in the observations and the manner in which they are recorded Inaccurate observations or mistakes made in recording may be worse than no observation since they lead to wrong conclusions regarding the performance of a strain Accuracy in making observations comes with experience and careful attention to details Notes recorded in a clear legible manner will reduce the number of errors Field notes are usually taken with a pencil of moderate hardness to prevent smearing and should be made in permanent notebooks.

3 *Simplicity* Any system of record keeping should be simple in its operation Otherwise the breeder will bog down in the detail of its upkeep and will fail to maintain up to date records The record system should be sufficiently simple for the breeder

Fig 5 14 Notes on various plant characters are recorded by the breeder from observations of maize varieties growing in the field

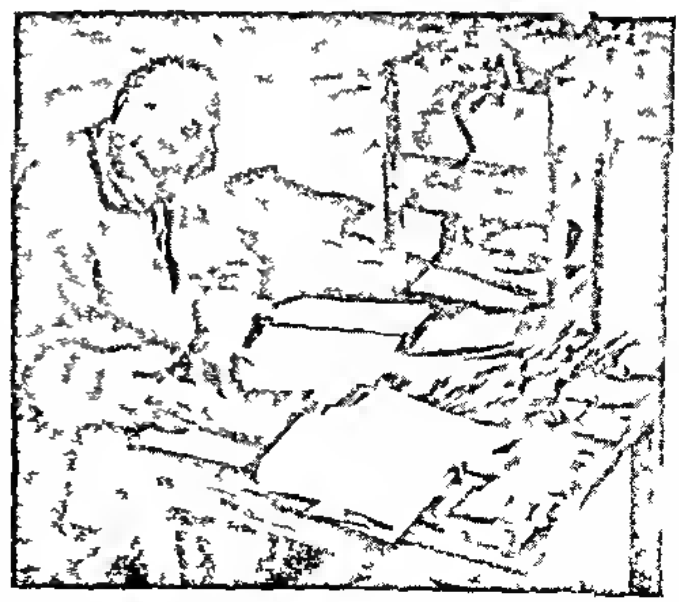


Fig 5 15 At the time of harvest seed samples are carefully labeled and observations on experimental materials recorded before they are placed in storage

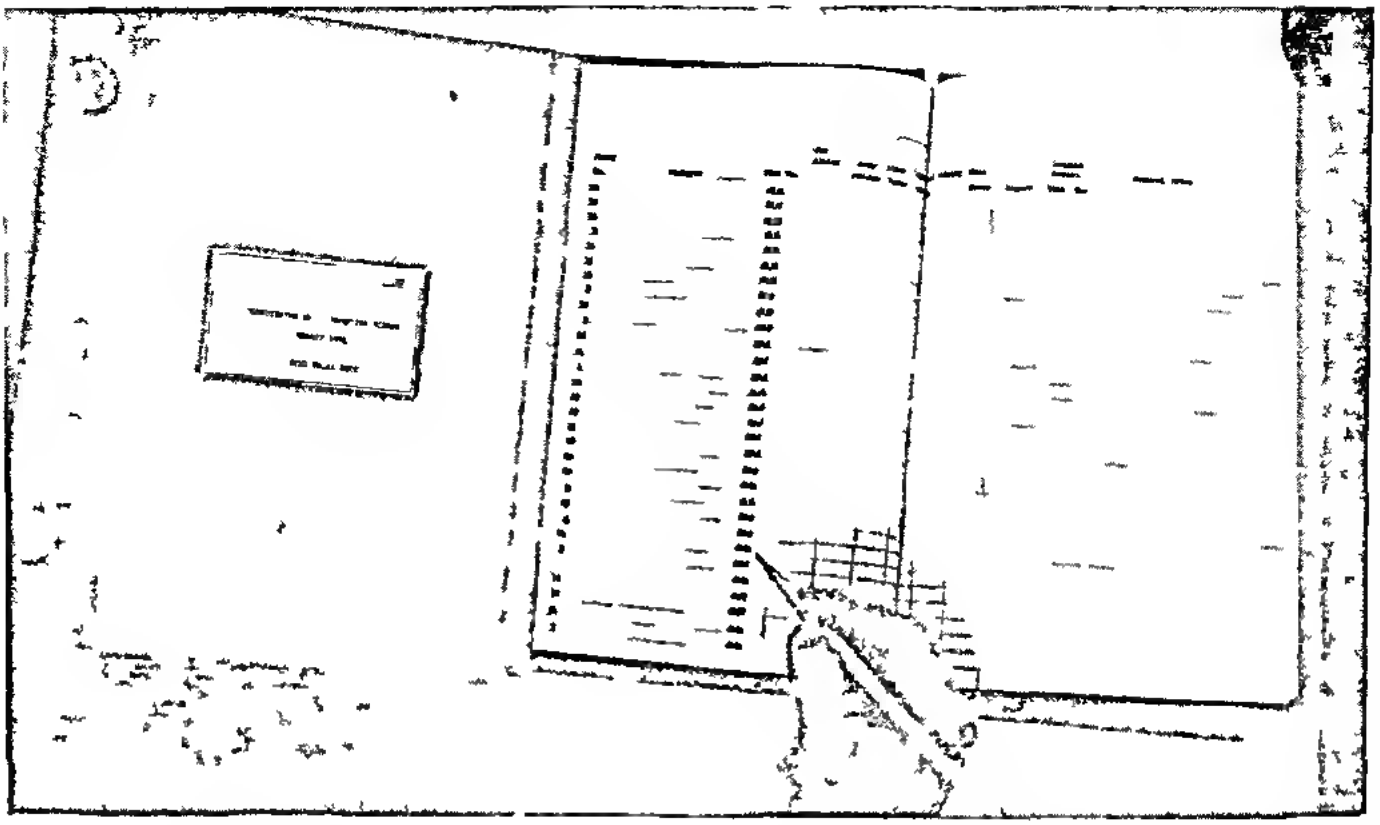


Fig 5 16 Field record notebook used in the Cooperative Maize Breeding Scheme in India Entries in yield trials are listed at left and column headings are labeled to facilitate recording of important observations in the field

or any of his helpers to be able to maintain it and to interpret the notes recorded

A few other observations that may be useful to the breeder in taking notes are

1 Every row or plot in the nursery should be easily and accurately identified by a row or plot number This is easily done by dividing blocks into ranges and by following a uniform system of numbering ranges and rows (or plots) For example, all plots within a block may be numbered by starting from a certain corner say the northwest, and proceeding from left to right

2 Adequate plot markers should be placed on a block so that the breeder or his helpers can find any plot quickly and easily Rows may be marked at regular intervals and if groups of related materials are planted together, a separate marker may be set to identify the first row of each group

3 Crosses and advanced strains may be given permanent accession numbers Each cross may be identified by a separate number, and selections from these crosses may be numbered so as to identify the year or generation selected All strains advanced into yield tests should receive permanent accession numbers

4 Permanent records may be recorded on standard notebook forms that are easily summarized For yield tests printed field notebook forms may be used with appropriate column headings according to the data to be recorded (Fig 5 16)

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6

Breeding Wheat

Wheat is the leading grain crop of the temperate climates of the world, just as rice is the leading grain crop in the tropics Although cultivated under a wide range of climatic conditions, the most extensive production of wheat is in areas where the winters are cool and the summers comparatively hot [44] In south and southeast Asia cultivation of wheat is concentrated in central, northern and northwestern India, roughly north of a line between Bombay and Calcutta and in Pakistan, where rainfall averages between 20 and 40 inches per year [40] In this area, the wheat is planted in the autumn and grows during the cooler and drier parts of the year, much of it under irrigation Very little wheat is grown in peninsular India, East Pakistan, Burma, Thailand and other countries of south and southeast Asia since the hot humid climate in these areas is unfavourable for good wheat production

India ranks fifth in acreage and seventh in production of wheat among all countries of the world Wheat ranks third in acreage and second in production among the other cereals grown in India The total production of wheat is about one third that of rice in India Uttar Pradesh, Madhya Pradesh, Punjab, Rajasthan, Maharashtra, Bihar and Gujarat are the most important wheat producing states in India

Wheat is unique as a world food grain because it contains a substance called gluten with physical and chemical properties which makes possible the production of a "risen" loaf of bread Wheat and to a lesser extent rye are the only cereals that contain gluten In addition to its principal use throughout the world in making bread, large quantities of wheat are used in making pastry and semolina products In India and Pakistan wheat is used for making chapatis The latter is a more common use of wheat than for making bread, especially in the villages in areas where wheat is grown

Genetic improvements in wheat have been taking place, both by the slow processes of nature and the selective processes of man, since the earliest time that wheat has been cultivated The bread wheats grown now represent the sum of all of these evolutionary changes The changes resulting from systematic breeding are largely confined to the past century Today, man is still changing the wheat plant with improvements in yield and in grain quality He is making wheat more resistant to drought, to lodging, to insects and to disease In this chapter we will study the methods by which these improvements are being made and the nature of the changes

ORIGIN AND GENETICS OF WHEAT

Wheat was already an important crop when history was first recorded and so accurate information on the exact time and place of its origin is not available [14] The distribution of the wild wheats and grasses, believed to be the progenitors of the cultivated wheats, supports the belief that wheat originated in southwestern Asia Some species were cultivated in Greece, Persia, Turkey, and Egypt in prehistoric times while the cultivation of other species may be of more recent origin In India, evidences from Mohen Jo Daro excavations, indicate that wheat was cultivated there more than 5,000 years ago [40]

The genetic origin of wheat is of interest for it is a classical example of how closely related species may be combined in nature into a polyploid series The species of *Triticum*, the genus to which the cultivated wheats belong, and their close relatives may be divided into diploid, tetraploid, and hexaploid groups, with chromosome numbers of $2n=14$, 28, and 42, respectively Representative species within each group are listed in Table 6 1 Species within the tetraploid group have apparently originated as

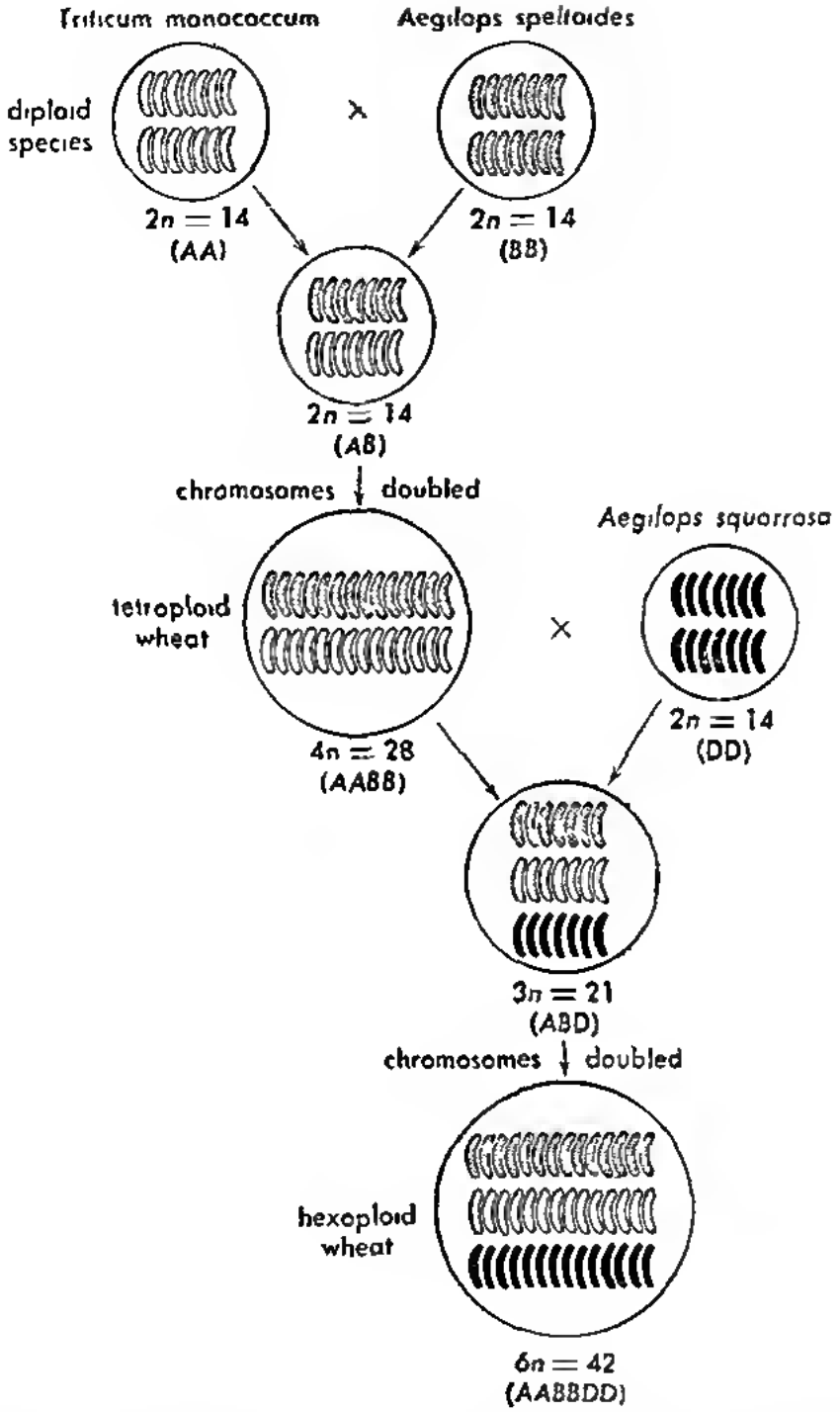


Fig 6 1 Origin of hexaploid wheat Tetraploid wheat originated as an alloploid from a cross between *Triticum monococcum* and *Aegilops speltoides* Hexaploid wheat originated by the addition of a third *genome* from *Ae squarrosa* or a close relative

Table 6.1 Genome Formulas for Several Species of Triticum and Some of Its Close Relatives[a]

Species	*Chromosome number (2n)*	*Genome formula*	*Common name*	*Use*
Diploid species				
Triticum boeoticum	14	*AA*	wild einkorn	wild
Triticum monococcum	14	*AA*	einkorn	cultivated
Aegilops speltoides	14	*BB*		wild
Aegilops caudata	14	*CC*		wild
Aegilops squarrosa	14	*DD*		wild
Secale cereale	14	*EE*	rye	cultivated
Tetraploid species				
Triticum dicoccoides	28	*AABB*	wild emmer	wild
Triticum dicoccum	28	*AABB*	emmer	cultivated
Triticum durum	28	*AABB*	durum wheat	cultivated
Triticum carthlicum	28	*AABB*	Persian wheat	cultivated
Triticum polonicum	28	*AABB*	Polish wheat	cultivated
Triticum turgidum	28	*AABB*	(solid stem) wheat	
Triticum timopheevi	28	*AAGG*	timopheevi	wild
Aegilops cylindrica	28	*CCDD*	goat grass	wild
Hexaploid species				
Triticum compactum	42	*AABBDD*	club wheat	cultivated
Triticum spelta	42	*AABBDD*	spelt	cultivated
Triticum aestivum	42	*AABBDD*	common wheat	cultivated

[a]Adapted from Sears[11] and Sarkar and Stebbins[12]

amphidiploids from two diploid species as indicated by the combinations of genome formulas (Fig 6.1). The hexaploid species originated by the addition of a third genome to a tetraploid species. Present evidence indicates that the tetraploid emmers (*AABB*) evolved from amphidiploids between *Triticum monococcum* (*AA*) and *Aegilops speltoides* (*BB*) or close relatives of these species,[52] and that the hexaploid wheats originated as amphidiploids between tetraploid emmers (*AABB*) and *Ae squarrosa* (*DD*) (Fig 6.1).[37, 55] A hexaploid wheat that closely resembles *T spelta* (*AABBDD*) and forms fertile hybrids with it has been synthesized from a cross between *T dicoccoides* (*AABB*) and *Ae squarrosa* (*DD*).[32]

The 21 chromosomes of hexaploid wheat (haploid number) have been assigned into seven homoeologous groups, each homoeologous group containing a partially homologous chromosome from each of the *A*, *B*, and *D* genomes.[13, 38, 59] This may be illustrated from the following grouping in which the chromosomes within each group are numbered 1 to 7 and the genome is indicated by the letter *A*, *B*, or *D*.

Homoeologous group	Genomes and chromosome number		
	A	*B*	*D*
1	1*A*	1*B*	1*D*
2	2*A*	2*B*	2*D*
3	3*A*	3*B*	3*D*
4	4*A*	4*B*	4*D*
5	5*A*	5*B*	5*D*
6	6*A*	6*B*	6*D*
7	7*A*	7*B*	7*D*

This system of numbering the chromosomes makes it possible to quickly identify both the genome and the homoeologous group to which it belongs

Chromosomes within a homoeologous group will carry many genes in common even though the chromosomes originated within a different genome The common genes indicate that the genomes at one time were probably derived from a common ancestor A large number of common genes within a homoeologous group would indicate a recent origin while fewer genes in common would indicate an earlier origin and that more evolutionary changes had occurred since the origin of the new species

It will be noted that we have referred to the 42 chromosome wheats as hexaploid wheats This is of course because they have originated by polyploidy and contain the diploid chromosome complements from three separate species In nature these wheats perform as diploids (n—21 and $2n$ 42) It has been shown that hexaploid wheats acquired this property of diploid pairing from a mutation on chromosome 5*B* which inhibits pairing between homoeologous chromosomes [49] [61]

Numerous inheritance studies have been made with the hexaploid and the tetraploid wheats However, many of the important agronomic characteristics with which the breeder works except for disease and insect resistance, are quantitative in nature and complex in inheritance Also, inheritance studies in common wheat are often difficult to analyze owing to the polyploid nature of the crop Many characters are dependent upon two or three genes, each gene having originated from a different genome As a result, progress in developing linkage maps of common wheat by conventional genetic methods was at first very slow More recently genetic studies in wheat have been facilitated by the development of *monosomics* (plants with one chromosome less than the normal) and *nullisomics* (plants with one chromosome pair less than the normal) in common wheat [56] [57] [68] By the use of these aberrant types the genetic analysis is simplified considerably, because a gene for a certain character can be positively identified with a specific chromosome For example, if a chromosome pair carrying a rust resistant gene is eliminated from a variety, the variety will no longer have resistance conferred by that specific gene By the use of these techniques more than 400 genes have been located in specific chromosomes These include genes conditioning important economic characters like black stem rust resistance,[60] brown leaf rust resistance,[20] yellow rust resistance,[62] and solid stems used in breeding for sawfly resistance [27] Uniform rules for nomenclature and symbolization of genes and gene symbols in wheats have been proposed [37] The rules are based on recommendations of the National Committee of Genetics and Breeding of the Science Council of Japan

The use of monosomics also facilitates the substitution of particular chromosomes with desirable genes from other varieties or from closely related species [68] [69] These techniques are proving to be useful tools for the plant breeder

POLLINATION IN WHEAT

Wheat is a self pollinating crop Blooming normally starts several days after the wheat spike emerges [29] The main culm flowers bloom first and the tillers later, in the order of their formation Flowering begins in the upper part of the spike and proceeds in both directions Flowering continues throughout the day with two to three days required for a spike to finish blooming The glumes normally open during the flowering process, the anthers protrude from the glumes, and part of the pollen is shed outside the flowers (Fig 6 2) Entry of foreign pollen while the flower is open may result in a small amount of cross pollination Normally, cross pollination is less than 1 percent If conditions are unfavourable for the opening of the glumes, the anthers may shed their pollen without being extruded To exclude all cross pollination in breeding or genetic studies the spike may be covered with a butter paper envelope prior to flowering

When two varieties are to be cross pollinated, flowers from the variety to be used as the female parent are emasculated and then pollinated with pollen collected from the male parent variety Wheat flowers are emasculated on the day prior to their shedding pollen by clipping back the glumes and removing the anthers with fine pointed tweezers (Fig 6 3, 6 4) Pollinations are made one or two days later by breaking a ripe anther over the stigma Crossing may be facilitated by the utilization of male sterile lines, thereby eliminating the emasculation process Genetic male sterility and cytoplasmic male sterility are both available in common wheat

TYPES AND VARIETIES

Wheat grain in world trade is classified commercially on the basis of texture, colour, growth

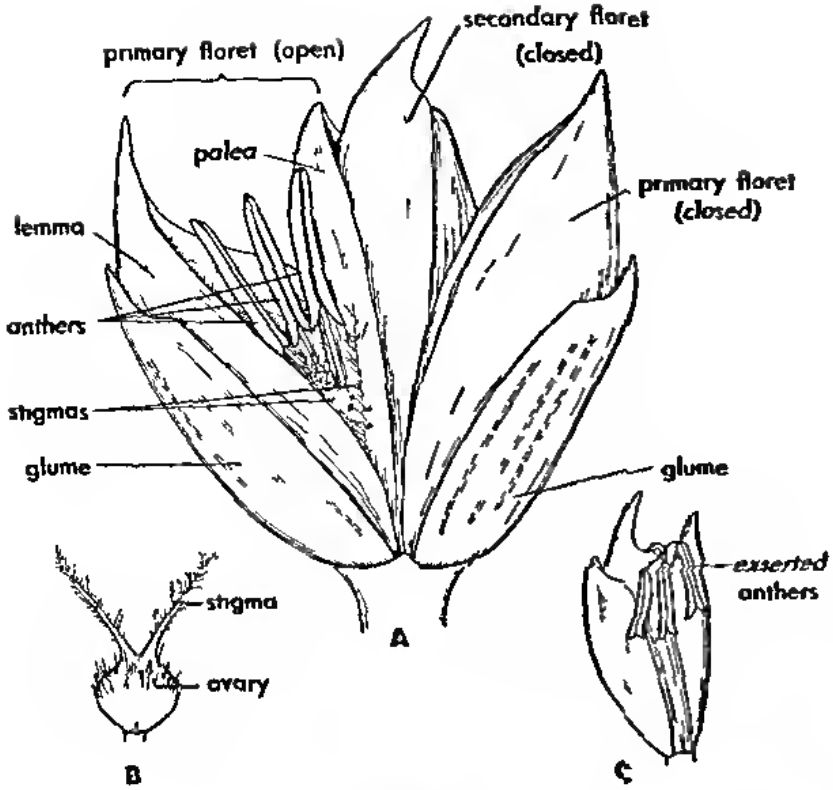
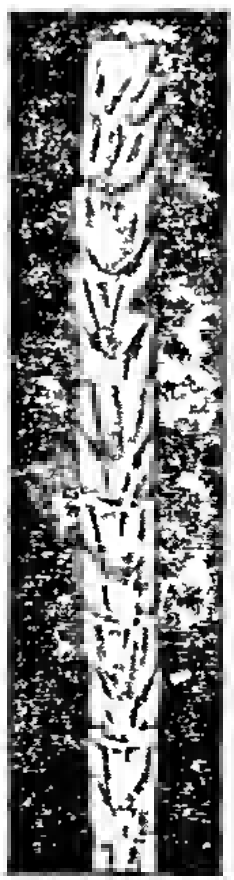
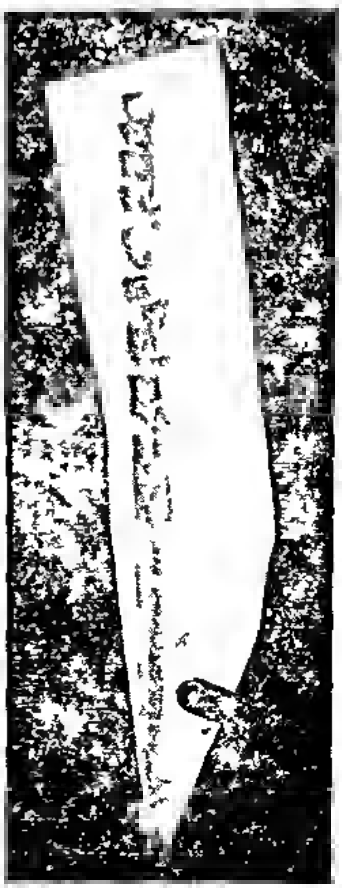


Fig 62 Spikelet of wheat A The primary floret on the left is open showing the three anthers and a port on of the feathery stigma The primary floret on the r ght and the secondary floret are closed B Pist l of wheat flower C Floret showing anthers exserted after blooming

Fig 63 Crossing wheat The wheat spike is emasculated by remov ng anthers before they shed pollen Ripe anthers from the pollen parent are transferred to the floret when the st gma becomes receptive



64A



64B

Fig 64 A Wheat sp ke with florets cl pped back to facilitate emasculation and crossing Glume and lemma have been removed from a floret on the right to show devel opment of stigma at this stage Anthers have already been removed B Wheat sp ke covered after emasculation to exclude fore gn pollen

habit of the plant, and other characteristics The exact system differs in different countries and for wheat grown in different areas But the objective of all commercial classification of wheat grain is the same, to reflect the utility of the wheat for a specific purpose The red and white-kerneled, hard textured wheats of *T aestivum* form the main bread wheats of world commerce In general these wheats tend to be high in protein and have strong gluten, which will produce a large loaf volume when the flour is baked into bread The red- and white-kerneled soft textured wheats of *T aestivum* and *T compactum* are used to a lesser extent for making bread and more extensively for making pastry products The soft wheats tend to be lower in protein and weaker in gluten, but these characteristics may be altered by the climate in which the wheat was cultivated and the variety grown The durums, belonging to the species *T durum*, include both red and amber kerneled types that are hard to vitreous in texture and are mainly used in the production of semolina products

In India five species of wheat are grown, *T aestivum* (bread wheat), *T durum* (macaroni wheat), *T dicoccum* (emmer wheat), *T sphaerococcum* (dwarf wheat), and *T turgidum* (rivit wheat) [40] By far the largest acreage of wheat grown in India and Pakistan is planted to the bread wheat, *T aestivum* The varieties grown mostly have white or amber kernels and hard texture, a type that is favoured for making chapatis and bread Some varieties with red kernels are also grown New semi dwarf wheats, recently introduced from Mexico have red kernels Durum wheat, *T durum*, occupies the second largest acreage It is cultivated in large areas of Madhya Pradesh Maharashtra, and Gujarat, under non irrigated conditons, because it is more drought resistant than the varieties of *T aestivum* The durum wheat is used principally for making chapatis Chapatis and bread made from durum wheat are inferior in quality to that made from the bread wheats *T dicoccum* is grown on less than one percent of the total acreage mostly in the states of Mysore, Andhra Pradesh, and Maharashtra *T dicoccum* is more rust resistant and will produce grain in areas with high incidence of black stem rust when the *aestivum* and *durum* wheats would fail *T dicoccum* is hard textured and is eaten mainly as a paste or gruel In general, white or amber wheats are preferred to red wheats in India for making chapatis Acreages planted to *T sphaero coccum* and *T turgidum* are negligible

Naming Wheat Varieties. Wheat varieties are generally designated by names through publication and usage The name may be a word—the name of a place, a man, or a descriptive term—a number, or a combination of words and numbers In India, wheat varieties are generally named by a letter indicating the experiment station or the state in which the variety originated followed by a number to designate the particular strain The early wheat breeding in India was done at an experiment station located in Pusa in Bihar State Wheat varieties originating at the Pusa station were designated by the letter P Examples of varieties developed there are P 4 and P 52 Later the station was moved to New Pusa near the city of Delhi, where it has developed into the present Indian Agricultural Research Institute Wheat varieties developed there are now designated by the letters NP (New Pusa) Examples are NP 770, NP 825, NP 836 Varieties originating from Punjab State usually have been designated by the letters C (cross) Examples are C 281, C 306 Various other letters or combinations of letters have been used in other states

The feeling is growing among many breeders that the use of letters and numbers should be abandoned in favour of short concise words not associated with the experiment station or state The arguments for this change are that words are easier to remember by the cultivator than numbers, and a variety with a wide adaptation should not have a name associated with a local area of adaptation

Cooperative Testing of Varieties. A Coordinated Wheat Improvement Scheme has been established in India The purpose is to promote cooperation among wheat breeders in various states and experiment stations in India by exchange of information, pooling of breeding materials, and cooperative testing of advanced strains prior to their release as new varieties To facilitate the testing, India has been divided into zones based on agroclimatic regions The programme is coordinated by staff members from the Indian Agricultural Research Institute, New Delhi, and the Rockefeller Foundation of India Breeders may enter elite experimental strains in zonal tests or in All-India tests, where they will be grown by other cooperating breeders in comparison with established

local varieties This cooperative testing programme enables the breeder to obtain information on the yield, adaptation, and disease resistance of new strains under a wide range of environmental conditions It also permits the breeder in one state to test and evaluate new strains from another state prior to their release and distribution as a new variety The performanee of new strains of wheat in these tests provides information upon which new variety releases and recommendations may be made

Before a new variety is distributed to the cultivators for production, the variety is named and seed of the new variety increased by the state or the experiment station developing it Before release as a new variety the strain should be proven to be superior to existing varieties in one or more important characters The superiority is proven by testing the new strain for at least 3 to 5 years, in comparison with the best adapted varieties, in local and regional trials Recommendation for release is made to the Central Variety Release Committee who officially releases the variety for production Breeder or nucleus seed is maintained by the experiment station developing the strain 'Breeder seed" supplied by the experiment station may be increased on district farms by the State Department of Agriculture or on cultivator's fields to produce 'Foundation seed' Foundation seed is then distributed for further increase and sale to cultivators Further information on seed production will be found in the chapter on Seed Production Practices

Varieties. Numerous varieties have been developed and released by the Indian Agricultural Research Institute and its various substations, and by the wheat research workers in the various State Agriculture Departments or the State Agricultural Universities Some varieties have wide adaptation and are recommended and grown over large areas Other varieties are recommended only for restricted areas or for specific growing conditions Variety recommendations may change from year to year as new varieties are released and as new research results become available For a list of varieties recommended for a particular area one should refer to the local agricultural experiment station or agricultural extension officer in the area concerned

METHODS OF BREEDING WHEAT

Systematic and organized research on the improvement of wheat in India by breeding was initiated by the late Sir Albert Howard and Mrs Howard at the Agricultural Research Institute, Pusa, Bihar in 1904 [40] Prior to this only limited work had been done in several states The breeding work started by the Howards led to the development of many excellent varieties [22] In 1936 the Pusa Institute was moved to New Delhi and work on breeding wheats is still being continued there in the Indian Agricultural Research Institute In 1907 research on the breeding and improvement of wheat was initiated at Lyallpur in the Punjab [2] Since 1947, Lyallpur is located in the new country of Pakistan where breeding work is still continuing Research on breeding is in progress at the Punjab Agricultural University, Ludhiana, and substations in the state of Punjab Breeding work is also in progress in Uttar Pradesh, Maharashtra, Madhya Pradesh, and other states in India In 1934 a programme for breeding rust-resistant hill wheats was initiated at Simla which is still continuing [43]

New wheat varieties may originate through (*a*) introduction, (*b*) selection, and (*c*) hybridization These methods of breeding self pollinated crops were discussed in Chapter 4 on 'Methods of Breeding Field Crops" Examples will be cited here of varieties which have been developed by each of these proeedures Examples will also be given of the use of the backcross, interspecific hybridization, and radiation in the development of new varieties as well as the potential utilization of hybrid wheat

Some Wheat Introductions. Introduction did not play an important part in the early breeding of varieties in India and Pakistan Foreign or exotic varieties imported by the Howards were mostly found to be too late in maturity for Indian growing conditions Therefore their early work was devoted largely to improvement of local strains This is in contrast to the U S A and Canada where wheat was not a native crop and where the breeding work has developed almost entirely from key introductions which have served as basic germ plasm sources One introduction into India that is grown extensively is the variety Ridley, introduced from Australia Ridley is fairly resistant to rusts, stiff strawed, and adapted to medium elevation hills of Punjab, Himachal Pradesh, Uttar Pradesh, and West Bengal [40]

Introductions have been used extensively in wheat hybridization programmes in India and

Pakistan as sources of genes for disease resistance Through hybridization the resistance genes have been transferred to adapted types and new varieties have been developed which combine the yield and quality of the Indian wheats with the resistance of the introduced variety Some introduced varieties which have been used as sources of disease resistance genes are Federation from Australia (resistance to loose smut) Thatcher from U S A Kenya E144 and Kenya E220 from Kenya, Gabo from Australia, and Gazin from Egypt (resistance to black rust), Frontiera, Frondoso and Rio Negro from South America, and Gazin from Egypt (resistance to brown rust), and Kononso from Japan and Spauldings Prolific, (resistance to yellow rust)

Recently several short strawed varieties have been introduced from Mexico which may greatly change the wheat variety pattern in India (Fig 6 5) These include Sonora 63, Sonora 64, Lerma Rojo and others These semi dwarf varieties, which have short, stiff straw, will stand without lodging when grown with irrigation and high rates of nitrogen fertilizer This feature of lodging resistance, combined with the ability to tiller profusely, enables the Mexican varieties to produce extremely high yields Under similar conditions of production, viz irrigation and high fertilization, Indian varieties would lodge so severely that grain production would be adversely affected (Fig 6 6) The Mexican varieties are red kerneled, a type not liked as well for chapati making as the white- or amber-kerneled varieties of Indian wheat

The origin of the Mexican wheats is an interesting story in plant introduction Following the second world war several short-statured Japanese varieties of wheat were sent to the United States of America for testing They were distributed by the United States Department of Agriculture to many of the states interested in wheat improvement In the state of Washington, Dr Orville Vogel crossed one of the short, semi dwarf Japanese varieties, Norin 10, onto a white local wheat, Brevor Semi dwarf selections from the Norin 10 x Brevor cross were later crossed onto red spring varieties by Dr N E Borlaugh in Mexico where the Rockefeller Foundation is assisting with the development of a wheat improvement programme Selections from the crosses made by Dr Borlaugh in Mexico as well as unselected hybrid materials were later introduced into India

Varieties Originating from Selection. It has already been mentioned that when the Howards started wheat improvement work in India at Pusa they had little success at first with foreign introductions, either used directly as varieties or as parents in crosses, since most introduced varieties were too late in maturity for the Indian climate. However, the Howards were able to develop within

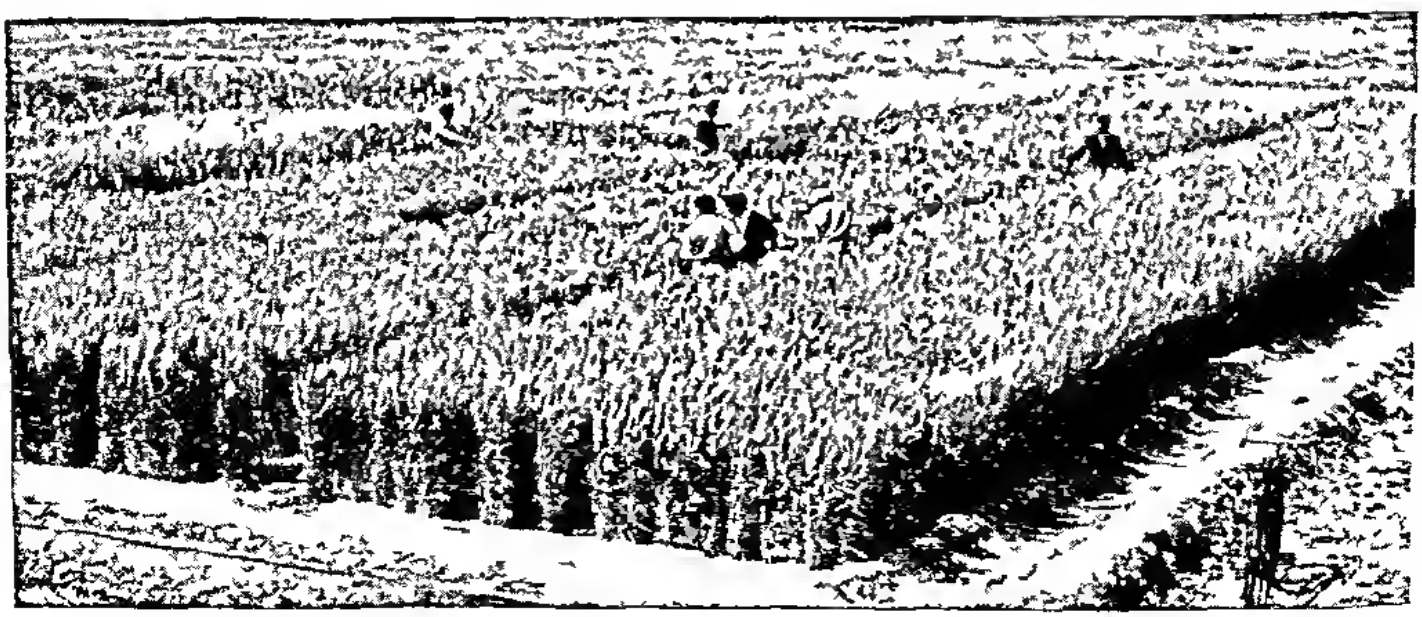


Fig 6 5 Portion of wheat breeding nursery at Punjab Agricultural University Ludhiana Varieties in foreground are semidwarf strains of Mexican origin

Fig 6 6 Comparison of height of new short lodging resistant strain of wheat of Mexican origin PV18 with a standard variety of Punjab C273

a short time several varieties outstanding in yield and quality by selection from local types Prior to the initiation of wheat improvement work in India various mixed types of wheat were being grown in the different areas the types being designated by local names Often hard and soft kerneled types or red and white kerneled sorts would become mixed with the result that price of Indian wheat on the export market was very low From these various types the Howards isolated many pure lines of which two became important and widely grown varieties Pusa 4 and Pusa 12 (now called N P 4 and N P 12) Pusa 4 has plump amber hard grains and Pusa 12 is a soft wheat with white grains

In the Punjab varieties selected from local types included Punjab Type 9 distributed in 1911 Punjab Type 11 distributed in 1913 and Punjab Type 8A distributed in 1919 Some of the other varieties selected from local types were Kanpur 13 and C 46 (Uttar Pradesh) AO 90 (Madhya Pradesh), and Bansi 168 and Bansi 224 (durums in Maharashtra state) Improvement by selection was possible in the beginning because the types grown by the cultivators were mixtures of many geno types But after the superior genotypes were isolated from these mixtures and grown as pure line varie ties further improvement by selection was limited

Varieties Developed by Hybridization Since about 1925 most of the important varieties of wheat developed in India have been developed by varietal hybridization After the superior selections had been isolated from the original local types it became apparent that important advances could not be made except by hybridization This sequence in obtaining new varieties is logical for an intelligent hybridization programme can be developed only after the parent materials have been sorted tested, and the best strains among them have been identi fied Also the large accumulation of knowledge in the field of genetics during the early part of this century made possible a clearer understanding of the mechanics and principles involved in combining the desirable characteristics of parent varieties through hybridization However, the practice of hybridization did not await a clarification of these principles for while not completely understood, hybridization had been practiced much earlier as the following examples will show

The Fulcaster variety of soft red winter wheat was produced in the U S A in 1886 by a farmer breeder S M Schindel in Maryland from a cross between Fultz and Lancaster [14] This variety was widely grown in the U S until a couple of decades ago

In Australia William J Farrer began an exten sive programme of wheat improvement in 1886 His most famous variety Federation produced in 1901 resulted from a three way cross involving Fife Etewah and Purplestraw Fife was introduced from Canada to give quality [14] Etewah an Indian variety was used to provide earliness Purplestraw was added to increase productiveness Federation was later introduced into India and crossed with Pusa 4 to develop the loose smut resistant variety, N P 165 Smut resistance in this cross was obtained from the Federation parent From successive crosses the loose smut resistance of Federation since has been contributed to a long line of Indian varieties

One of the earliest varieties to be developed by

hybridization in India was N P 52 N P 52, which originated from the cross Pusa 6 × Punjab 9, became widely grown in northern India [40] In 1934 a rust resistant breeding programme was initiated at Simla and hybridization has since been used extensively to combine genes for rust resistance from introduced varieties with high yield and good quality of adapted Indian varieties From this programme and from the breeding programme in the Punjab have come such varieties as N P 710, N P 718 N P 737, N P 770, N P 797, N P 809, N P 846 C 253, C 273, C 285 C 286, C 306 and many others [40]

Varieties Developed by the Backcross. The backcross method of breeding new varieties was pioneered and used intensively at the California Agricultural Experiment Station in the U S A There it was used in the systematic improvement of several varieties by adding, through a succession of crosses to the recurrent parent, single genes from a donor parent For example genes for bunt resistance rust resistance, and hessian fly resistance have been successively added to the variety Baart by the backcross procedure described in the chapter on Methods of Breeding [10] The result has been the development of (*a*) a bunt resistant variety of Baart, (*b*) the development of a bunt and stem rust resistant variety of Baart, (*c*) a red kernel variety of the bunt and stem rust resistant Baart, and (*d*) intensification of the stem rust resistance and Baart-like characteristics The varieties produced, the pedigrees, and the purpose of the crosses are listed in Table 6 2. In naming the backcross derived varieties, the name of the recurrent parent, Baart, has been used throughout, to which has been added the year in which the variety was released or distributed For example 'Baart 35" is a backcross improved Baart distributed in 1935 The newly developed varieties are quite similar to the original Baart strain except for the character added by the backcross procedure

The backcross procedure used here is desirable when one has a suitable adapted variety which may be used as the recurrent parent to which the breeder desires to add a dominant monogenic character As shown, more than one character may be added by pursuing simultaneously several backcross programmes and merging the final results of each Sometimes it is desirable only to intensify the genes for a specific quantitative character which is inherited in a polygenic manner rather than recover the entire genotype of the recurrent parent For this one or two backcrosses only may be used The backcross method generally has been used very little in the wheat breeding programmes in India except in the latter manner

Table 6.2. Backcross Improvement of Baart Wheat in California[a]

Variety	*Pedigree*	*Purpose of cross*
Baart 35	Martin × Baart^{-b}	add bunt resistance to Baart
Baart 38	(Hope × Baart^{5}) × Baart 35	add bunt and stem rust resistance
Baart 46	Baart 38 × Baart^{2}	greater stem rust resistance and more Baart like
Baart 52	(red selection from Baart 38 × Baart 38^{2}) × Baart 46	red kernel colour
Baart 54	Baart 46 × Baart^{2}	very Baart like strain

[a] After Briggs and Allard [10]

[b] Superscript refers to number of crosses to the recurrent Baart parent variety For example Baart^{7} refers to the original cross and six backcrosses to the Baart parent variety

Composite Crosses. Composite crosses, in which selected varieties are crossed and pairs of F_1's successively crossed until all enter into the final parentage, offer an opportunity to bring together innumerable genetic combinations This procedure was used in barley and is the basis of Suneson's "evolutionary" method of breeding A variation in this procedure is to utilize male sterility to obtain random crossing between genotypes in the original crosses and in succeeding generations This procedure was used in the U S A in the production of a composite cross in wheat [67] Pure lines may finally be isolated from the composite cross population after segregation has virtually ceased

Multiline or Composite Variety The concept that multiline or composite varieties may have wider adaptation and greater usefulness than single line (pure line) varieties has received much consideration in recent years The advantages and objections to multiline varieties were listed in Chapter 4 A procedure that has been proposed

for developing a multiline or composite variety with rust resistance is as follows [8]

1 Choose a commercially acceptable variety for the recurrent parent
2 Introduce, concurrently, different genes for rust resistance into the recurrent variety by separate backcross programmes
3 Composite 5 to 10 different backcross derived lines of the recurrent variety each with a different gene for rust resistance
4 Increase the composite and grow as a commercial variety

New backcross derived lines of the recurrent parent variety may be developed as new genes for rust resistance are identified The new lines may be entered into the composite at any time to replace lines which become susceptible due to new physiologic races of the rust organism arising

A huge effort toward the development of multiline varieties is being made in the Mexican wheat breeding programme under the leadership of Dr N E Borlaug of the Rockefeller Foundation [8] The multiline approach is being made with the belief that losses from airborne diseases such as rust will be reduced if greater genetic diversification for rust resistance is introduced into a variety In a multiline variety the build up of rust inoculum on susceptible component lines will be more slowly than if the entire variety is susceptible As a result, possible subsequent development of a rust epidemic will also be delayed and less loss will occur even to the susceptible component lines This breeding procedure is based on the assumption that all genotypes in the multiline variety will not become susceptible to a new race of the rust organism at the same time

Interspecific and Intergeneric Crosses. Interspecific and intergeneric crosses involving common hexaploid wheats and species at the tetraploid level may be used to transfer desirable genes, such as rust resistance, insect resistance, and other characters from the tetraploid species to common wheat In the U S A , stem rust resistance genes were transferred from Yaroslav emmer to the Hope variety and from Iumillo durum to the spring wheat variety, Thatcher, a gene for resistance to the insect pest, hessian fly, was transferred from the Portuguese durum, P I 94587, to common wheat, and wheat like selections were obtained from crosses of common wheat with *Agropyrum elongatum* that are resistant to wheat streak mosaic and to wheat joint worms In India genes for rust resistance from Khapli emmer have been used in breeding for rust resistance An intergeneric cross involving the use of x rays to assist in the transfer of a leaf rust resistance gene from the diploid species, *Aegilops umbellulata*, to common wheat[58] was described in Chapter 3 Other species closely related to common wheat have also been used as sources of desirable genes for wheat improvement

Mutation Breeding. Radiations and chemical mutagens may be used to increase mutation frequencies in wheat as in other crops The most common observable mutations following radiation have been speltoids, compactoids, sub-compactoids, awn mutations, chlorophyll mutations and other abnormalities undesirable to the breeder [7] These may generally be classed as macromutations and are often accompanied by sterility and other undesirable pleiotropic effects In addition, many small micromutations occur the effects of which are not visible on single plants but can be measured in a population of plants The micromutations may be more useful than macromutations in breeding since they are less likely to be accompanied with pleiotropy or sterility Sterility following radiation may result in outcrossing if plants are unprotected from foreign pollen Offtype plants selected from advanced generations of irradiated populations may therefore be a result of mutation plus outcrossing

An awned mutant, N P 836 was selected following irradiation with x rays of the variety N P 799 at the Indian Agricultural Research Institute The mutant strain closely resembles the parent in other morphological characters grain shape, quality, and rust resistance [42] The awn character is monogenic in inheritance

Two varieties of wheat Lewis and Stadler have been developed at the Missouri Agricultural Experiment Station in the U S A by mutation breeding Both varieties were selected following irradiation with thermal neutrons of an improved experimental strain Lewis is shorter and stiffer-strawed, and Stadler is higher in yield and test weight and has more resistance to leaf rust than the parent strain It is not known whether the changes observed are the direct result of alterations in the genic materials following radiation or whether genic alterations and outcrossing have both occurred The latter appears to be the most plausible explanation

The two varieties were named after Dr Lewis J Stadler who in 1928 at the Missouri Station was the first to demonstrate that exposure to ionic radiations would increase the mutation rate in plants

Irradiation with x rays was utilized at the Missouri Agricultural Experiment Station in the U S A to obtain a crossover between a wheat chromosome and an alien chromosome from *Aegilops umbellulata* which resulted in the transfer of a gene for leaf rust resistance from *Ae umbellulata* to common wheat [58] This was described in Chapter 3 (Figs 3 19 and 3 20)

Germ Plasm Collections Large collections of wheat varieties and genetic stocks are maintained in many countries with wheat breeding programmes Most extensive collections are probably those in the U S A and the U S S R The Food and Agricultural Organization of the United Nations is maintaining a World Catalog of Genetic Stocks of Wheat in which are found descriptions agronomic characteristics and information on disease and insect resistance on several thousand strains as well as the address of the person or organization maintaining the genetic stock

Hybrid Wheat Heterosis in yield and other characters in wheat have been observed for many years [9 41] Utilization of hybrid vigour as a method in breeding wheat became possible after finding cytoplasmic male sterility and pollen restoring genes in the wheat plant The cytoplasmic sterility sterilizes the wheat pollen thus permitting natural cross pollination instead of self pollination as normally occurs (Fig 6 7) Pollen fertility is restored to the hybrid wheat by dominant fertility restoring genes contributed by the pollen parent

Cytoplasmic male sterility in wheat was first discovered during the 1950 s by Japanese scientists

6 7A

6 7B

Fig 6 7 Cytoplasmic male sterility in wheat. A Spikelet of male sterile wheat with open florets The florets remain open until pollinated B Spikelet of normal male fertile wheat. Florets open briefly at anthesis and anthers are extruded

who crossed tetraploid durum and hexaploid bread wheats to related wild grasses. At the Fort Hays Kansas Agricultural Experiment Station in the U.S.A., two plant scientists, Wilson and Ross, in 1962 reported that stable cytoplasmic male sterile forms of wheat had been obtained by crossing the hexaploid hard red winter bread wheat variety, Bison, to *Triticum timopheevi* Zhuk (2n=28).[74] In 1963, it was reported that male fertility restoring genes were present in a derivative of a bread wheat × *T. timopheevi* cross that would restore fertility to the cytoplasmic male sterile Bison.[31] Fertility restoring genes which gave complete fertility restoration to cytoplasmic male sterile Bison were also reported from crosses of *T. timopheevi* with Marquis, a variety of hard red spring wheat, in 1967.[30] These discoveries, *cytoplasmic male sterility* and *male fertility restoring genes*, provide the tools needed to implement the production of hybrid wheat on a commercial basis.

Breeding and utilization of hybrid wheat involves three steps (*a*) development and maintenance of male sterile lines, (*b*) crossing of male steriles with fertility restoring lines, and (*c*) utilization of these in the commercial production of hybrid seed. Each will be discussed.

A. DEVELOPMENT AND MAINTENANCE OF MALE STERILES. The original cytoplasmic male sterile Bison was developed by crossing *T. timopheevi* × Bison, selecting for partially male sterile plants, and successively backcrossing the sterile plants to Bison as the recurrent pollen parent until fully male sterile lines were obtained and the genotype of Bison recovered. The backcross procedure is similar to that outlined in Chapter 4. The objective is to transfer the chromosomes of Bison, a variety of *T. aestivum*, into cytoplasm of *T. timopheevi*. Since cytoplasm contributed to the embryo comes from the egg, the pollen grain being so small that it contributes an insignificant portion of cytoplasm, *T. timopheevi* is used as the female parent in the original cross, and male sterile or partially male sterile plants selected from the progeny of each cross are used as the female plants in successive backcrosses. Normal or male fertile Bison is used as the recurrent pollen parent in the original cross and each of the backcrosses. The final product of these crosses is a cytoplasmic male sterile variety identical to the normal or male fertile Bison in all respects except for having aborted anthers and failing to produce viable pollen. By a similar procedure of crossing and backcrossing using the male sterile Bison as the female parent in the backcrosses, other varieties of hexaploid wheat may be sterilized, providing they do not carry pollen restoring genes. Normally 5 to 7 backcrosses, using the variety to be sterilized as the recurrent pollen parent, are required to transfer the chromosomes to the sterile cytoplasm.

The cytoplasmic male sterile varieties are maintained by pollinating them with a male fertile counterpart (Fig. 6.8). For example male sterile Bison, known as the A line, is pollinated by normal Bison, known as the B line. The progeny from this cross will be a male sterile Bison. The male sterility of Bison has been proven in a wide range of environmental conditions. However, it has been observed that some varieties when sterilized may be fully sterile in some environments yet may produce some fertile pollen in other environments. This emphasizes the need for testing each male sterile line carefully in all areas where it may be used in a commercial wheat hybrid.

B. CROSSING MALE STERILES TO FERTILITY RESTORING LINES. Hybrid wheat is the F_1 progeny of crosses between two selected parent lines. In the production of hybrid wheat one parent will be the cytoplasmic male sterile A line produced by the procedure described above. The pollen parent, known as the R line (Fig. 6.8), will be one that (*a*) restores fertility in crosses with the male sterile A line, and (*b*) nicks with the A line to produce a vigorous and productive F_1 hybrid. The fertility restoring genes may be transferred to a wheat variety to be used as an R line by the backcross procedure described in Chapter 4. Male fertility in cytoplasmic male sterile wheats with *T. timopheevi* cytoplasm may be restored by the presence of two dominant genes, Rf_1 and Rf_2.[30] These genes were identified in a plant selected from the cross *T. timopheevi* × Marquis.[3] Presumably these genes are present in *T. timopheevi*, for without these or similar genes the *T. timopheevi* wheats would not produce fertile pollen.

In the production of hybrid wheat the A line contains sterile cytoplasm and recessive genes for fertility restoration, hence it is male sterile. The B line contains recessive genes for fertility restoration but has fertile cytoplasm, hence it is male fertile. The R line will have the dominant genes for fertility restoration, Rf_1 and Rf_2, but may have either sterile cytoplasm (from *T. timopheevi*) or fertile

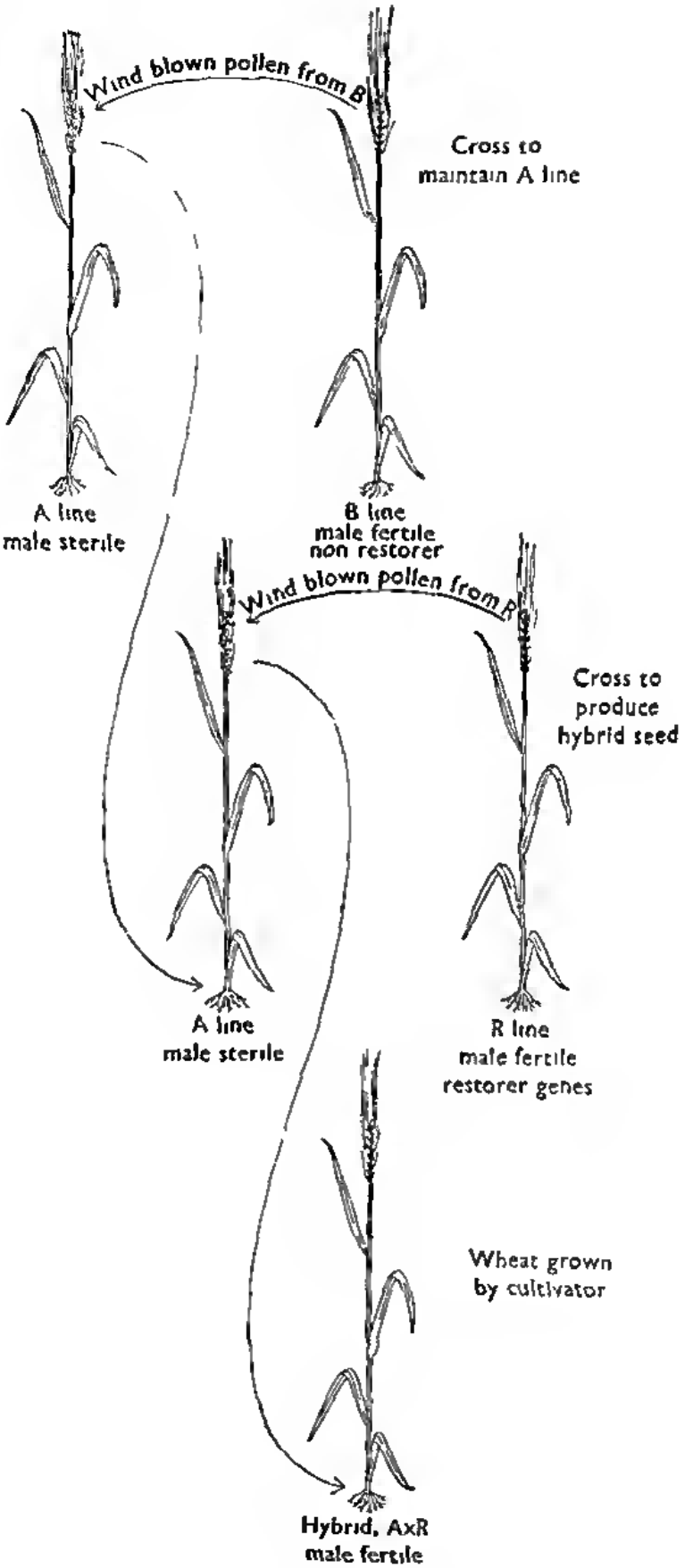


Fig 68 Scheme for the production of hybrid wheat by utilizing cytoplasmic male sterility and fertility resorting genes

cytoplasm (from *T aestivum*), in either case it will be male fertile. It may be easier to develop restorer lines with sterile cytoplasm than with fertile cytoplasm since the presence of the *Rf* restorer gene will be apparent then without test crossing onto male sterile lines. The cytoplasmic and genic content of the lines utilized in breeding hybrid wheat with the *timopheevi* cytoplasm is shown in Table 6.3.

C. PRODUCING HYBRID WHEAT. In the beginning of the hybrid wheat programme standard varieties or experimental lines will be converted either to male sterile A lines or to fertility restoring R lines and used in the production of hybrid wheat. Present evidence indicates that yield increases in the magnitude of 25 to 30 per cent over the average of the parents may be expected from appropriate variety crosses of currently available materials. The yield level of wheat hybrids in relation to parent varieties may be expected to be increased as research advances and new lines are developed with superior combining ability. Current research indicates that 50 to 60 per cent seed set in seed production fields may be expected under favourable conditions for pollination with a ratio of 1 male pollinator row to 2 female hybrid seed producing rows.[75] More experience is needed in seed production procedures to determine finally the ratio of seed producing to pollinator rows to plant, the conditions for obtaining maximum seed set, and other details which will affect the economy of hybrid wheat seed production. Experience is also needed to learn which varieties may be converted to male sterile A lines and which may be used as fertility restoring lines. Since it will not be possible to convert varieties or lines with male fertility restoring genes to male steriles, the latter presumably may be converted to male fertility restoring R lines. Much breeding and testing is also required to develop and identify the lines that will combine to produce high yielding F_1 hybrids with acceptable agronomic type and baking quality. It is also necessary that the A lines and the R lines flower at the same time in order that cross pollination is effected.

OBJECTIVES IN WHEAT BREEDING

The ultimate goal of the wheat breeder is to develop new varieties improved in some important features. This goal can be reached only by carefully planned selection and hybridization procedures which lead toward well established and clearly defined objectives. The breeder needs to know what improvements will increase the productiveness and quality of wheat varieties and thus will be useful and profitable to both grower and processor. He must search out parent materials superior in these features and combine the good characteristics into a superior variety. The objectives of wheat breeding are not always the same, for the environmental conditions that affect wheat production and adversities that limit wheat yields differ from one production area to another. However, certain broad objectives are important over wide production areas. These include (*a*) yield of grain, (*b*) maturity, (*c*) standing ability, (*d*) drought resistance, (*e*) disease resistance, (*f*) insect resistance, and (*g*) quality. The utilization of these objectives in a breeding programme will be discussed.

Yield of Grain. Yield of grain is important for it measures the total returns to the wheat grower. Yield is affected by all of the environmental conditions influencing the growth of the wheat plant as well as the plant's heredity. The inherent capacity

Table 6.3 Cytoplasmic and Genic Content and Pollen Fertility of Lines Utilized in Breeding Hybrid Wheat

Wheat Material	*Cytoplasm from*	*Fertility restoring genes*	*Pollen fertility*
A line	*T timopheevi* (sterile)	rf_1rf_1 rf_2rf_2	Male sterile
B line	*T aestivum* (fertile)	rf_1rf_1 rf_2rf_2	Male fertile
R line	*T timopheevi* (sterile)	Rf_1Rf_1 Rf_2Rf_2	Male fertile
or	*T. aestivum* (fertile)	Rf_1Rf_1 Rf_2Rf_2	Male fertile
Hybrid	*T. timopheevi* (sterile)	Rf_1rf_1 Rf_2rf_2	Male fertile

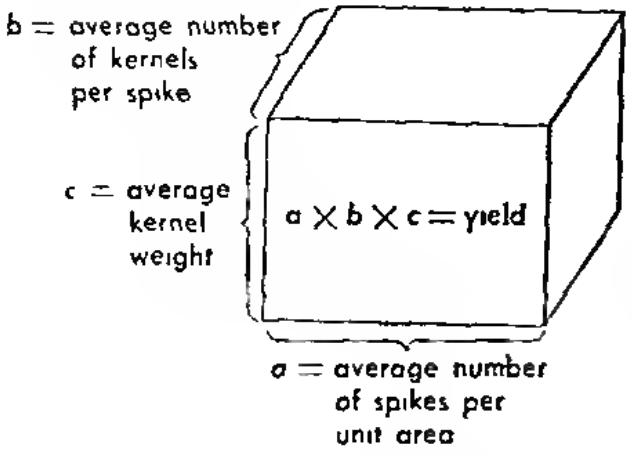


Fig 69 Yield per unit area may be represented geometrically as a box, the volume of which will be dependent upon the number of spikes per unit area, the number of kernels per spike, and the average kernel weight

for yield may be expressed through such morphological features of the plant as tillering, length and density of the spike, number of grains per spikelet, or size of the grain But no one of these physical components of yield can by itself be considered as an index to yield Some high yielding varieties may have long spikes and only moderate tillering capacity Other varieties equally high in yield may have high tillering capacity and short spikes It has been suggested that yield of a small grain variety like wheat and oats can be likened to a box [17] To represent the three dimensions of the box we may use (*a*) the number of heads per unit area, (*b*) the number of grains per head, and (*c*) the average weight per grain (Fig 69) The volume of the box, which will be the yield of the variety, is determined by the product of these components An increase in any one of the three components would result in an increase in total yield, provided there is no corresponding decrease in the other two components With this representation of yield the problem of breeding for higher yield becomes that of finding the inherent combination of the three components that will result in the greatest volume of the box In practice, as one component of yield is increased, the others tend to decline As tillering capacity is increased, the heads tend to become shorter, or the size of the grains may be reduced Thus selection cannot be made for one component without full consideration of the others

Yield of a variety of wheat is measured in kilograms of grain per hectare Inheritance of yield is complex and quantitative The ability to yield is expressed through the photosynthetic and metabolic processes within the plant Perhaps we should say that the yield capacity of a variety is its inherent ability to synthesize starch, proteins, and other food materials, and to translocate and store them in the grain If the breeder is to increase one component of yield of grain without reducing the other components by a corresponding amount, it will be necessary to increase the efficiency of many vital processes within the plant This means of course that, since many complex physiological processes within the plant are influencing yield, many genes affecting the functioning of these processes must contribute to the final production of the grain Since individual genes affecting complex yield processes cannot be identified, all of them are often lumped together by the breeder and referred to as "yield genes" *Thus to breed for high yield it is necessary to combine into a variety a favourable combination of yield genes*

All this is assuming that the wheat plant has a favourable environment in which to grow, that no factor such as heat, moisture, or disease will limit the final yield To find such an environment would be rare indeed So the ability of the plant to produce well in spite of an adverse environment will also contribute to the final production of grain Thus we breed for resistance to a particular disease in areas where that disease is limiting production, or for resistance to heat, or drought, or insect damage A variety of wheat with resistance to stem rust might yield more than a susceptible variety in the presence of a heavy stem rust epidemic, even though the resistant variety was less productive in the absence of the rust The ability of the wheat to stand until harvested without loss of grain from lodging or shattering will also affect the final yield, as well as its ability to mature within the limits of a favourable season While constantly striving to improve

potential yielding ability by grouping into one strain of wheat the more favourable combination of yield genes, *it is also necessary to stabilize production by breeding for resistance to the many adversities that may limit the final harvest*

In countries like U S A and Canada where harvest is mechanized tall growing wheats with high straw yield are undesirable The excess straw not only contributes to lodging but it also impedes the harvest operation In India and Pakistan good yields of straw are important to the cultivator as well as good yields of grain Here the straw is needed for cattle feed, for thatching, and other uses The development of short statured wheat which can utilize high doses of fertilizer without lodging is sometimes looked on with disfavour by the cultivator if they also result in lower yields of straw However, the loss of yield due to less height will usually be made up by the higher tillering ability when the higher fertilizer applications are made Also, the higher grain yields will more than compensate for the loss in yield of straw In India and Pakistan increased foodgrain production is essential to feed the growing population It will not be possible to realize maximum grain yields of wheat without growing short strawed varieties which will stand under irrigation and respond to high fertilizer applications So development of short strawed varieties with high tillering capacity must be a major objective in a wheat breeding programme

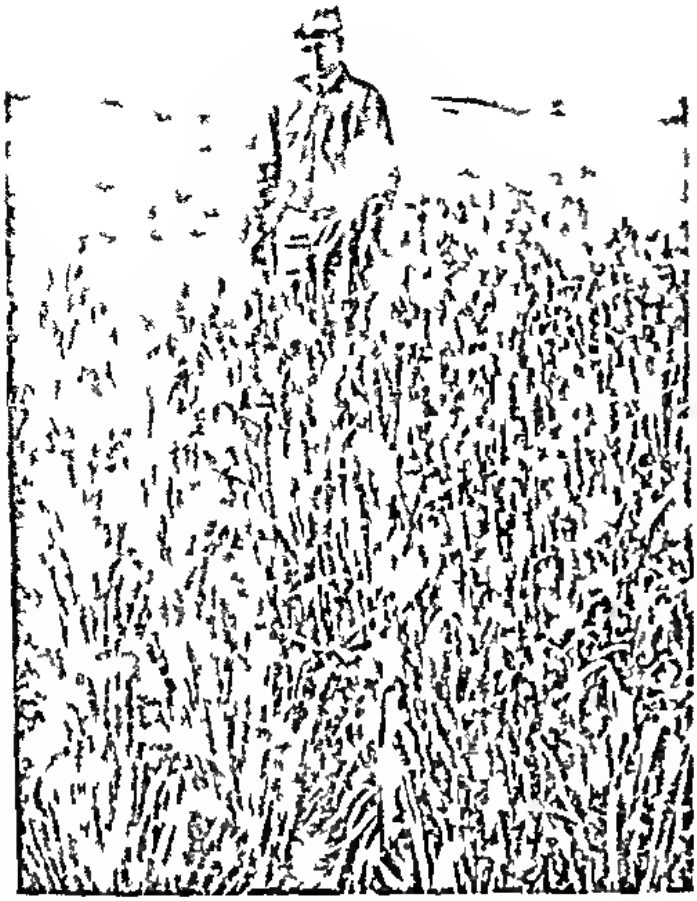
Maturity. In the central and northern Plains of India and Pakistan wheat has a relatively short growing period Wheat is planted in late November or December and is harvested from late February in Maharashtra or Madhya Pradesh to April or May in Punjab and Pakistan Growth is restricted and maturity hastened toward the end of the growing period by high temperatures and low soil moisture Varieties tend to mature very quickly after earing begins In the northern Plains, the cooler temperatures during the winter months tend to provide a long period of tiller formation and a relatively short period for ear formation and filling of kernels In the central Plains, where the winter temperatures are higher, as in Maharashtra and Madhya Pradesh, the period for tiller formation is reduced Under these conditions early varieties are grown to escape the heat and drought It will be recalled that the early work of the Howards in introducing foreign varieties to India was unsuccessful as the introduced varieties were too late in maturity In the development of Federation wheat, Farrer in Australia used Etewah, an Indian wheat, as a parent in his 3-way cross to contribute earliness Varieties developed in India with extremely early maturity include N P 165, N P 771, N P 797 and N P 798 The newly introduced Mexican wheats are also early in maturity

In the hills of north India the growing conditions are somewhat different from the Plains The winter temperatures are much cooler and less growth occurs during this season Ear formation and kernel filling occur later than in the Plains Varieties adapted to the Hills generally do not perform well in the Plains and *vice versa*

The advantages of early maturity are many (Fig 6 10) It enables the wheat to escape some of the ill effects of the hot summer weather drought and rust It permits an early harvest thereby releasing the land for another crop Most early wheats have shorter straw and are less likely to lodge There are also certain disadvantages of earliness Early wheats tend to be lower in yield because the wheat plant has a shorter growth period in which to tiller, bloom, and to manufacture and store food materials in the wheat kernel It has been demonstrated however, that it is possible to obtain favourable combinations of genes for both yield and earliness within the same variety Varieties in the U S A, such as Monon, Knox and Triumph, are both early and high yielding The Mexican varieties introduced recently into India are also early and high yielding

The inheritance of earliness is complex and apparently depends upon the specific varieties being crossed For example, in a cross between two spring varieties, multiple inheritance (three factors or more) was reported with earliness at least partially dominant In a cross between Kawvale and Early Premium varieties of winter wheat, lateness was reported to be dominant with three factors involved in the inheritance of maturity [45]

Standing Ability. The ability of a wheat variety to stand in the field until harvest without loss of grain is important in obtaining a high yield The application of higher rates of fertilizer amendments, especially nitrogen, and the use of mechanical harvesters in most important wheat growing areas of the world, have increased the need for the breeder to improve varieties in standing ability



Fg 6 10 Comparison of ma ur y n wheat The stram at right has already started to head Dr S P Kohl Co ordinator of he All Ind a Whea Impro emen Programme s ands n he background

The standing ab l ty of the wheat plant involves its resistance to lodging and its resistance to shatter ing These will be d scus ed separately

A LODGING RESISTANCE Lodging in wheat occurs as a result of the bending or breaking of the wheat culm [16] Losses from lodg ng occur with any of the following condit ons

(*a*) The wheat lodges before it is ripe and does not fill properly
(*b*) The fallen wheat is not completely picked up in the harvest and is left in the field
(*c*) The lodged wheat provides a favourable environment for the development of rust, mildew or other diseases

Ra n ha l and windstorms occurring after the wheat has headed but before it ripens are common causes of lodging (Fig 6 11A) The wheat at this stage is green and heavy and is easily bent or broken

Lodged 6 11A Not Lodged

Resistant 6 11B Suscept b e

Fg 6 11 Comparat ve lodging in wheat varieties A Lodging from wind and rains orm before the wheat was r pe B Lodging due to disease Straw of the suscept ble var ety was weakened by stem rust

over by the added weight of the rain or the force of the wind Addition of irrigat on water at this stage may soften the soil and reduce the effectiveness of the root anchorage to such an extent that the

wheat will lodge Plants that are merely bent over may rise upright again after they have dried off, with little reduction of final yield But if the culm is broken, the spike does not fill normally or may be lost entirely Breakage of the culms at this stage of development may reduce the final yield by 20 to 30 per cent [28] Kernel weight and protein content are also reduced Plants with culms which are inherently weak or plants which are very succulent as a result of excessive nitrogen fertilization or soil moisture will be more susceptible to lodging injury Resistance to lodging may be improved by the development of varieties with (*a*) stiff, sturdy stems, (*b*) short straw, (*c*) a vigorous root system that will anchor the plant firmly in the soil, (*d*) more resilient straw that will not break in the wind, and (*e*) resistance to diseases and insects that weaken the straw or the root system

Lodging may also occur after the wheat is ripe and before it can be harvested Delay in harvesting as a result of continued rainfall will result in this overripened wheat bending over Eventually the culms may break Development of varieties with short, stout stems will increase the length of time the wheat will stand without breaking Some varieties are inherently stronger than others, even though the diameter of the culm may be similar This is apparently associated with the structure of the cells and the deposition of lignin in the cell wall The brittleness of the straw is also important since some apparently stiff strawed varieties break under the pressure of strong winds

Disease and insect damage may result in lodging, as when the wheat straw deteriorates from a stem rust infection, (Fig 6 11B), or breaks over from damage by stem borers or hessian fly Presence of root rots may also result in lodging of the wheat plant, for the anchorage of the plant will be weakened Breeding for resistance to these diseases and insect pests will increase the ability of the wheat plant to stand in the field until harvest without lodging

Breeding for high yield and breeding for lodging resistance must go hand in hand With advanced practices in cultivation high yields cannot be attained without application of large doses of commercial fertilizer, especially nitrogen New varieties of wheat must stand without lodging when given heavy fertilizer applications or high production of grain will not be obtained and the investment on fertilization will be largely wasted This means that *new varieties of wheat must be short strawed and stiff-strawed* so that they will not lodge The high yielding Mexican wheats introduced into India are short and stiff strawed and produce high yields of grain when fertilized without lodging Present day Indian varieties are much improved in lodging resistance over older varieties but are mostly too tall to be grown with the high fertilizer applications required for production of maximum yields Short straw has the additional advantage that less straw will need to be handled in the harvesting operation thus reducing the cost of harvesting and threshing This is particularly important in countries where mechanical harvesters are used

The short straw of the Mexican wheats originated from crosses made in the U S A, Canada, and Mexico with a short strawed variety, Norin 10, from Japan [72] Lodging resistance of varieties can be compared by growing them in the field with irrigation and high nitrogen fertilization, conditions favourable for inducing lodging in weak-strawed varieties In the laboratory various techniques such as the breaking strength of the straw may be used to compare the relative straw strength of different varieties [26]

Since the nature of lodging resistance is so complex its inheritance is also complex However, inheritance studies may be simplified somewhat by separating components contributing to lodging resistance—short straw, culm size, culm structure, root development, disease resistance, and others—and studying the inheritance of each separately Apparently the short stature of the Mexican wheats, inherited from their Norin parentage, is relatively simple Dwarf and semidwarf wheats of this type are generally referred to as 1 gene dwarfs, 2 gene dwarfs, or 3 gene dwarfs, according to the number of major dwarfing genes they contain The wheats with 3 major dwarfing genes are the shortest and usually these are also reduced in yield The 1-gene dwarfs are grown as commercial varieties Minor genes modifying the effects of the major genes may also be present

B SHATTERING RESISTANCE Losses from shattering usually occur when harvesting is delayed after ripening, especially if wheat ripens in periods of hot, dry weather Varieties of wheat differ in their tendency to shatter [12 18] The varieties with greater shattering resistance tend to have a larger amount

of lignified tissue at the breaking point of the outer glume [71]

Drought Resistance About three fourths of the wheat cultivated in India are grown under rainfed conditions without supplemental irrigation [40] Wheat is planted at the end of the rainy season and except for occasional winter showers receives little or no precipitation during its period of growth The plant makes the heaviest drain on the soil moisture during the period from flowering to seed maturity This growth period comes at the beginning of the summer season when soil moisture supplies are severely depleted and temperatures high This condition places a severe drought stress on wheat grown under rainfed conditions Even with irrigation, temporary drought stress may occur during periods with high temperatures and high transpiration Under prolonged drought stress the growth and maturation periods of the plant are shortened severely Many of the older land or native varieties of India are able to survive this stress better than the newly developed varieties which have been derived by hybridization with exotic or foreign varieties The variety C 591 developed in Punjab has superior drought resistance Most introduced varieties perform very poorly when subjected to extreme drought stress Varieties may also differ in heat resistance which intensifies drought stress [51]

Evaluation of drought resistance is difficult Perhaps the best criterion is yield of grain when the varieties are grown in critical drought situations Ability to retain green colour and a succulent turgid condition is associated with drought resistance The leaves of the introduced Mexican wheats quickly turn white under extreme drought stress Early maturing varieties tend to escape drought damage This is important in the adaptation of early varieties to India and Pakistan Durum wheats are grown in the rainfed areas of the central Plains because they are earlier and more drought resistant than varieties of common wheat Drought resistance is a complex characteristic and, like lodging resistance, its inheritance is also complex

Disease Resistance. The development of varieties of wheat with resistance to destructive diseases has been among the foremost contributions in wheat breeding In a breeding programme each disease must be considered as a separate problem Inheritance of many diseases is relatively simple being conditioned by 1 or 2 major genes In India, excellent progress has been made in breeding wheat for resistance to black or stem rust, brown or leaf rust, yellow or stripe rust, and loose smut. Resistance genes for each of the three kinds of rust and for loose smut first were separately incorporated into adapted varieties By a succession of crosses between varieties already resistant to one disease, resistance to two or more diseases within the same variety was obtained Later, by multiple crosses resistance to several diseases have been combined into single varieties Other diseases of economic importance include bunt, mildew and *Alternaria* leaf spot Problems involved in the breeding of these diseases will be discussed

A BLACK OR STEM RUST *Puccinia graminis tritici* (Pers) Erikss and Henn Stem rust is one of the most destructive of plant diseases (Fig 6 12) [15] The fungus inciting stem rust spends part of its life cycle on species of *Berberis* It also may spread in the uredo cycle from one wheat plant to another, the uredospores being carried by the wind This seems to be the way in which the stem rust organism is propagated in India The summer heat destroys the spores in the plains but the rust may over summer on volunteer or early sown summer crops of wheat or barley in the hills of north India The spore infections are then carried down to the foot hills and finally to the plains [33]

Black stem rust has been a serious disease of wheat over India for many years To combat this menace a programme for breeding rust resistant hill wheats was started at Simla in 1934 The purpose was to combat the disease at the source and thereby reduce the spore showers drifting down from the hills to the plains [43] From this programme many new rust resistant varieties of wheat both for the hills and for the plains have been developed [70] This work has been carried out largely by the cooperative efforts of the plant breeders and mycologists in the Departments of Botany and Mycology of the Indian Agricultural Research Institute, Delhi, and their substations located at Simla (Punjab), Bhowali (U P), Pusa (Bihar), Indore (Madhya Pradesh), and Wellington (Nilgiri Hills) Rust resistant strains for Punjab are also being developed at the Punjab Agricultural University, Ludhiana

The breeding of wheat varieties resistant to black stem rust is complicated by the fact that the organism inciting black stem rust (*Puccinia gra*

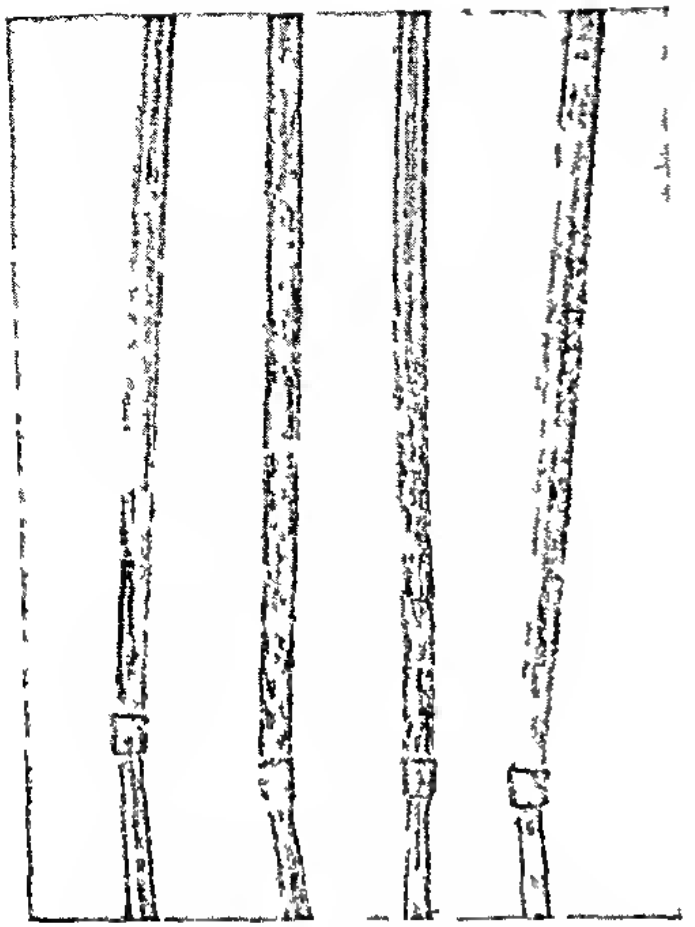


Fig 6 12 Stem rust on wheat Stem rust causes premature ripening severe lodging and reduction in yield and bushel weight

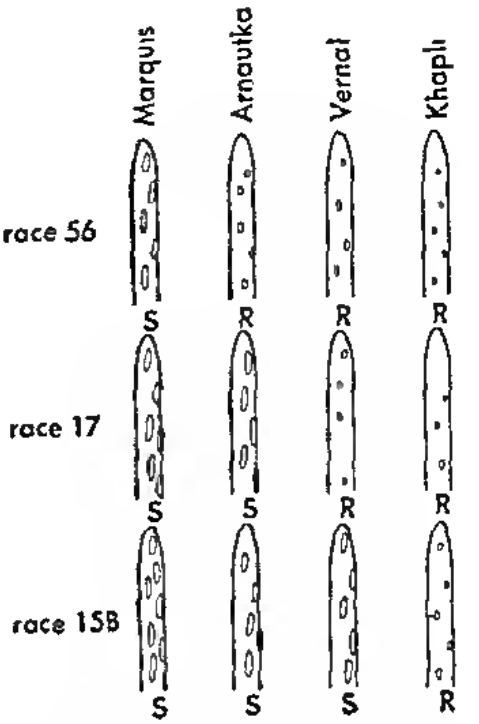


Fig 6 13 Seedling reaction of four differential wheat varieties to three common races of stem rust (*S*=susceptible, *R*=resistant)

minis tritici) has numerous physiologic strains or races [64] Each race of the stem rust organism differs from other races just as varieties of wheat are inherently different One of the races of rust may infect certain varieties of wheat, but not others This is another way of saying that a variety of wheat may be resistant to certain races of rust, but not others The races of rust are morphologically similar, but pathologically different The races are identified only by the response or reaction of the varieties of wheat to infection About 300 distinct races of stem rust have been identified by the differential reaction of a few varieties[66] (Fig 6 13) New races of rust commonly originate by hybridization between present races or by mutation, just as new varieties of wheat are developed A new variety of wheat may be resistant to those races of stem rust that are prevalent in nature at the time of its distribution, but new races, to which the wheat variety is susceptible, may arise and become widespread Then the "resistant' variety may be attacked by the new races

Breeding stem rust resistant varieties is a continuing process because the rust race complex continues to change [19 65] As new races of rust appear which infect commercial varieties, genes for resistance to the new races must be searched out and incorporated into adapted strains [19 73] It is necessary for the breeder to know which races of stem rust are widespread to learn about the new races that are increasing in nature, and to find varieties resistant to them The infection pattern of stem rust races and wheat varieties was first worked out at a "rust laboratory" established cooperatively by the United States Department of Agriculture and the Minnesota Agricultural Experiment Station Hundreds of collections of stem rust from the United States, Canada, and Mexico were examined each year at this laboratory and the physiologic race or races of each collection were identified Recently "International Rust Nurseries" have been grown around the world, in which the resistance of wheat varieties to prevailing races of black stem rust may be studied With these nurseries

Table 6 4. Reactions to Four Physiologic Races of *Puccinia graminis tritici* of the Thirteen Wheat Varieties Used to Differentiate Races of Stem Rust

Variety	Species	Reaction[a] to physiologic race number 56	17	11	15B
Little Club	*Triticum compactum*	S	S	S	S
Marquis	*Triticum aestivum*	S	S	S	S
Reliance	*Triticum aestivum*	S	R	S	S
Kota	*Triticum aestivum*	S	S	S	S
Arnautka	*Triticum aurum*	R	S	S	S
Mindum	*Triticum durum*	R	S	S	S
Spelmar	*Triticum durum*	R	S	S	S
Kubanka	*Triticum durum*	S	S	S	S
Acme	*Triticum durum*	S	S	S	S
Einkorn	*Triticum monococcum*	R	S	S	S
Vernal	*Triticum dicoccum*	R	R	R	S
Khapli	*Triticum dicoccum*	R	R	R	R
Lee	*Triticum aestivum*	R	R	R	S

[a]S=susceptible, R=resistant

the potential resistance of a new variety throughout the world is soon learned

Twelve varieties of wheat are used to differentiate the races of stem rust [66] In addition, the variety Lee is often used to differentiate between race 15 and 15B The reactions of these "differential" varieties to four races—56,17,11, and 15B—are given in Table 6 4 Whether a variety is resistant or susceptible to a specific raec may be determined by the intensity and nature of the infection that the rust pathogen incites in the wheat plant (Fig 5 12) The severity of the infection is also affected by the temperature of the atmosphere and the age of the plant Some varieties are resistant at low temperatures but not at high temperatures Some varieties are resistant both in the seedling stage and as mature plants, while others are resistant only after maturity Many of the races of stem rust are actually mixtures of genetic types and may be further subdivided into subraces or biotypes if tested on additional differential varieties The 13 'international differential" varieties have been used to identify the races of black stem rust collected in India By 1965, 13 races and 5 biotypes of the black stem rust organism had been identified from collections made in India [46] From the annual identification of races it has been seen that the prevalence of some races fluctuate widely in India Race 15, the most common race before 1938 has almost disappeared and race 21, which was rare before 1942, has become the most prevalent One of the races present in India, race 122, is a virulent race to which sources of resistance are difficult to find

The resistance of a variety of wheat to a particular race of stem rust can be determined only by growing the variety under conditions where it will be exposed to an attack of that race of the rust organism and observing the number, size, and character of the rust pustules that develop (Fig 5 12) The severity of the disease is generally expressed as a percentage of the maximum possible infection Since rust does not occur in the field every year artificial rust epiphytotics are frequently established in a disease nursery where the varieties and strains are growing Wheat varieties may also be tested in the glasshouse for their rust reaction Inoculations in the field may be made by injecting a suspension of rust spores into the leaf whorl of a susceptible "spreader variety" early in the season The rust spreads from the spreader variety into adjacent rows of the selections or varieties being tested In the glasshouse, rust spores are usually rubbed or dusted on wheat plants (Fig 5 11) growing under temperature and humidity conditions favourable for germination of the spores and the development of the rust By use of artificial inoculations, a variety may be tested with known races of rust, and thus information about the reaction of the variety to specific races of the rust organism may be obtained

No variety of wheat is known to be resistant to all races of black or stem rust Earlier, interspecific crosses were used extensively in the U S A to transfer genes for resistance to black or stem rust to common wheat Some of the sources used were Yaroslav emmer (used in Hope variety), Vernal emmer (used in Carleton and Stewart durum) and Iumillo durum (used in Thatcher) Later, wheats originating in Kenya in Africa were used In India, Thatcher was used as a source of resistance in early crosses but proved to be susceptible to

certain races Khapli emmer has been used in crosses with durum wheats Recently, the variety, Kenya E220, has been used extensively as a source of resistance to black stem rust

The inheritance of resistance varies with the variety being studied and the specific race of rust with which the variety is inoculated For example, resistance in Hope was reported to be due to one or two dominant genes, although other workers indicated additional genes were involved Kenya 58 has been shown to have a gene governing resistance to race 15B [24] Gabo, Lee, and Timstein have two complementary genes governing resistance to race 56 [24] Using monosomic analysis, two recessive duplicate genes for resistance to race 15C in the variety N P 790 were found to be located in chromosomes 1A and 2A [63] Other modes of inheritance have been reported with other parent varieties

B BROWN OR LEAF RUST *Puccinia recondita* Rob ex Desm Brown or leaf rust is found regularly in the hills in India but occurs only occasionally in the plains or peninsula The organism inciting leaf rust, like that inciting stem rust, has many physiologic races About 200 races have been identified in the U S A [23] The prevalence and distribution of the races are constantly changing as new virulent races develop and become widespread Many races of leaf rust, like those of stem rust, could be subdivided into biotypes or subraces if additional varieties were to be used as differentials The breeder must know the races present in his area when selecting a source of resistance Fifteen races and one biotype of brown leaf rust have been identified in India[46] using the ' international differential host" varieties Varieties of common wheat which have been used as sources of leaf rust resistance include Mediterranean, Democrat, Exchange, Frontana, Rio Negro, Timstein, and others Genes for resistance to leaf rust have been transferred to common wheat from *Triticum durum* (2n=28), *T timopheevi* (2n=28) *Aegilops umbellulata* (2n=14), and other species

The mode of inheritance of resistance to leaf rust may vary from one to several genes and depends upon the parent variety [1 20 48] As with stem rust, inheritance studies are influenced by the races of rust present, the stage of plant growth, and other factors Artificial epiphytotics of leaf rust may be established in the field or in the glasshouse The methods are similar to those used for establishing artificial epiphytotics of stem rust

C YELLOW OR STRIPE RUST *Puccinia striiformis* West This rust develops under cooler conditions than the other rusts and so it is a greater menace in the northern hill areas where temperatures are lower It is seldom found in the plains of peninsular India but is sometimes found in the hills of Madras Eleven races of the yellow rust organism have been identified in India [46] High resistance to yellow rust was obtained in the variety N P 770, the resistance genes coming from the variety Konoso, an introduction from Japan Other varieties used as sources of resistance include Cometa Klein, Frondosa, Le Prevision and Frontiera The inheritance of resistance is dependent upon the resistant parent variety and the race of the rust used For example, resistance of La Prevision to race 13 was controlled by a single dominant gene In the cross Frondosa ×N P 770, resistanee to race 13 was due to a single pair of recessive genes The resistanee of Frontiera to race H of yellow rust in a eross with N P 770 was due to the aetion of duplicate reeesive genes [35] Using monosomic analysis, Cometa Klein was reported to have one recessive gene on each chromosome 4A and 6A which together control resistance to race H, and one recessive gene on chromosome 5A [62]

D LOOSE SMUT *Ustilago tritici* (Pers) Rostr Loose smut is a common disease in most wheat growing areas [15] The fungus inciting loose smut is borne inside the seed and heat treatment of the seed is required for its control Sinee the heat treatment is difficult to manipulate the use of resistant varieties offers the best means of control

Several physiologic races of loose smut have been described in the U S A [5 6] but no studies have been made of the race situation in India Breeding for resistance was begun at an early date in India The resistance of Australian Federation was transferred to N P 165 in the cross Pusa 4 × Federation Most of the wheat varieties released in recent years possess resistance to loose smut.

Resistant strains are identified by their freedom from smutted plants after being subjected to natural infection or to artificial inoculation The artificial inoculations are usually made by injecting dry spores or a spore suspension into the florets at the time of flowering The smut reaction is usually expressed either as the percentage of smutted heads

or as the percentage of smutted plants One, two, and three genes have been reported for resistance in different varieties [31]

E HILL BUNT *Tilletia fœtida* (Wallr) Liro and *T caries* (DC) Tul Hill bunt occurs in the hilly areas of north India, where it may cause serious losses to the crop As with the rusts the breeding of resistant varieties is complicated by the occurrence of a large number of physiologic races [50] More than 13 races of *T fœtida* and 12 of *T caries* have been identified in 50 bunt collections from India and Nepal [46] From 70 wheat varieties tested 8 introduced or exotic varieties were found to be resistant In the U S A and Canada various varieties, including Rio, Oro, Hussar, Ridit, Florence, Martin, Rex and Hope have been found resistant and used in bunt resistant breeding programmes Wasatch and Brevor developed in the U S A were resistant also in India [36] Hussar has been reported to have a single dominant gene for resistance when tested with Indian collections of bunt [25]

Five major genes for resistance to specific races and two weak genes have been identified as follows Martin *MM* and M_2M_2, Hussar *HH*, Rio *RR*, Turkey *TT*, and the weak genes *XX* and *YY* [11] Five of these genes, *MHRTX*, are associated in the same linkage group [53] The Rio gene (*RR*) and the Turkey gene (*TT*) are closely linked and react similarly to the different races The Martin gene and either the Turkey or Rio gene together give resistance to twenty five races of *T caries* and *T fœtida*

Wheat may be tested for resistance to bunt by dusting the seed before planting with the smut chlamydospores Infections are reported as per cent of smutted plants

F KARNAL OR PARTIAL BUNT *Neovossia indica* (Mitra) Mundkur Karnal or partial bunt is found in cooler areas of Punjab and Uttar Pradesh The disease, which is air borne, does not occur regularly Breeding for resistance has received little attention in India

G POWDERY MILDEW *Erysiphe graminis tritici* E, Marchal Powdery mildew may cause serious losses in the hills of north India and is sometimes found in other areas Many physiologic races of the organism inciting powdery mildew occur Resistance has been identified in varieties of common wheat but breeding for resistance has received little attention in India

H LEAF BLIGHT *Alternaria triticina* Prasada and Prabbu This leaf blight disease is incited by a newly identified species of *Alternaria* The disease causes severe damage to wheat in Maharashtra, Bihar and West Bengal Sources of resistance have not been identified [47]

Insect Resistance. Breeding for resistance to insects has been given much attention in the U S A and Canada where varieties resistant to the hessian fly stem sawfly, and green bug are being grown [31] In India and Pakistan there have been no serious insect problems although nematodes, white ants and stem borers may sometimes cause injury No breeding work for resistance to insect pests is now in progress in these countries Stored grain pests may cause damage to wheat in storage Hard kerneled varieties resist damage by these pests more than varieties with soft kernel texture

Quality. In breeding for high quality the breeder must give consideration to the physical and chemical characteristics of the wheat kernel that will affect its utilization [3 4] All of the objectives considered thus far either directly or indirectly affect the yield or production of the variety In directly some of them may also affect quality Quality is generally of little concern to the cultivator, unless the poor quality adversely affects the price that he receives in the market Seldom does he receive a premium for superior quality Here, we must distinguish between market quality and milling or baking qualities of wheat varieties The first is largely affected by the environment in which the wheat is grown and only secondarily by its inheritance Milling and baking qualities are usually primarily affected by the inheritance of the wheat.

A MARKET QUALITY Wheat of good market quality must be pure, clean, and sound, for these characteristics determine, within limits, its market value These features of the wheat grain may be affected by the method in which the crop is produced For example, if the wheat becomes contaminated with undesirable crop or weed seeds damaged by the weather before harvest, or spoils in the bin after being stored, the market quality is impaired Such reductions in quality could not have been alleviated by breeding In general, varieties that produce good yields within their area of adaptation will also produce grain of satisfactory market quality However, the wheat crop may be poorly filled and light in weight as a result

of lodging or rust damage Breeding varieties with stiff straw or rust resistance would then prevent loss in quality from these causes Unadapted varieties, those too late in maturity for example, may have shriveled kernels and low bushel weight All of these characteristics are expressions of market quality

B MILLING AND BAKING QUALITIES The milling and baking quality of a variety is dependent upon its use In India, wheat is used largely for making chapatis For chapatis, grain appearance—colour, size, and texture—are given primary consideration (Fig 6 14) White or amber grains, medium large to bold in size, with hard vitreous texture and lustrous appearance appeal to the consumer and are given preference White or amber kernels give a uniformly white flour Red kernels give a dark or discoloured flour Mottled kernels (alternately hard and soft) are likewise disliked Varieties should have uniformly hard, lustrous kernels even under irrigation All of these characteristics are based on visual observations of the wheat kernel and quality evaluation of new wheat varieties in the past has been almost entirely on these visual characteristics Adjustments for quality variations in the wheat can usually be made by manipulations during the grinding of the flour, mixing of the dough and baking of the chapatis all hand processes

Wheat used in baking bread is subjected to numerous physical and chemical processes during the milling and baking procedures Since many of these procedures are mechanized, they are less subject to manipulations which may adjust for quality differences in the wheat It is important therefore that the wheat milled into flour and baked into bread possess those milling and baking qualities that will result in the production of a uniform flour and finally a uniform and acceptable loaf of bread [21] As the economy of India and Pakistan advances, there is likely to be greater utilization of the wheat for baking bread than at present This will require that more emphasis be placed by the breeder on milling and baking quality

Recently a cereal quality testing laboratory was set up in the Indian Agricultural Research Institute, New Delhi, with primary concern for evaluation of wheats and other cereals for industrial utilization (Fig 6 15) [3] Preliminary studies have been made on procedures for evaluating wheat for chapati making [24] Procedures for evaluating wheat for baking bread are more widely known [21] Some of the tests commonly employed determine such properties as percentages of protein and ash, viscosity, mixing time, water absorption, loaf volume, and others The details of the tests are too complex to elaborate here

The wheat breeder needs information about the milling and baking properties of the new varieties and strains that he develops so that he will not distribute a variety with unsatisfactory quality [4] In the past he has depended largely on visual observations In the early stages of selection only small amounts of seed are available for quality tests While baking tests are the final measure of quality, they require too much grain and are too

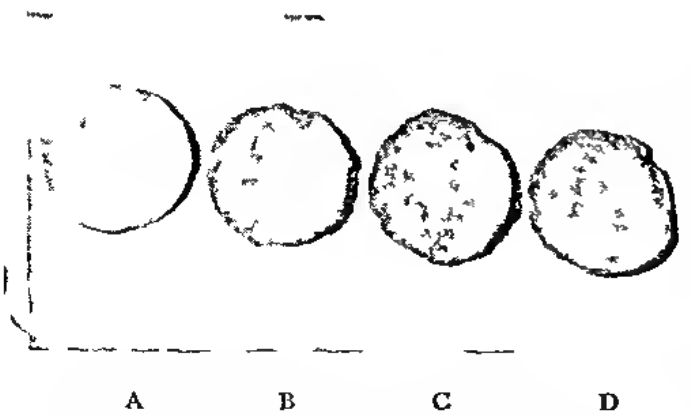


Fig 6 14 Chapatis baked from A High quality pearly grain Indian variety of bread wheat (*T aestivum*), B *Durum* wheat (*T durum*), C *T dicoccum* D Red winter, Mexican variety (*T aestivum*)

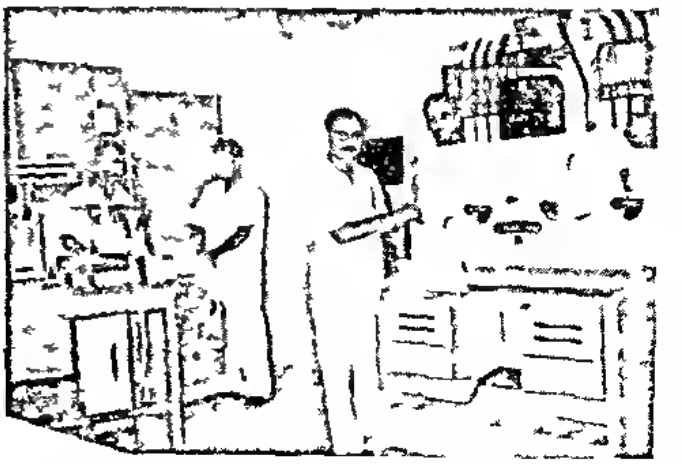


Fig 6 15 Cereal quality testing laboratory at Indian Agricultural Research Institute, New Delhi At right is an experimental mill for milling small quantities of flour from wheat varieties grown in varietal test plots

expensive to be used except with the elite strains that have been advanced for final yield testing Development by the cereal technologist of preliminary screening tests, employing simple microtechniques and requiring only small amounts of grain, aids the breeder by permitting him to test the quality of the strains in the early stages of breeding Currently the laboratory at I A R I is evaluating entries in the All India Coordinated Wheat Testing Programme

Quality is a complex characteristic Its inheritance, like the inheritance of yield, is extremely complex

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7

Breeding Rice

Rice is the principal food crop and the cereal grown most extensively in the tropical and subtropical regions of the world. Over 85 percent of the world's rice is grown in China, India, Japan, Pakistan, southeastern Asia, and the adjacent islands of the Pacific. China and India produce around 50 percent of the world rice supply, while another 25 percent is produced in Japan, Pakistan, Indonesia, Burma, and Thailand. Brazil is the leading rice producing country outside of this area.

ORIGIN OF RICE

Rice is one of the oldest cultivated crops and has been cultivated in China and India for several thousand years. The cultivated species of rice, *Oryza sativa*, is thought to have originated in south and southeast tropical Asia because it is in this area that there is found the greatest diversity of the cultivated forms.[4 11 55] The only other cultivated species of rice, *O. glaberrima*, is grown in west tropical Africa, and is indigenous in that area.[4] There are widely divergent views regarding the progenitor of cultivated rice but the consensus of opinion favours the view that it originated from the species complex known as *O. perennis*.[10 11 41] A polyphyletic origin of the *Oryza* species from several ancestral types is generally accepted.

In addition to the two cultivated species there are a number of wild species in the genus *Oryza*, the exact number is not yet settled. Several workers have proposed 23 species but others recognize as many as 28 species of *Oryza*.[11 14 32 55 60 62] *O. sativa* is the only species to be found in both tropical and temperate regions, all other species of *Oryza* being found in tropical areas only. The interrelationship of the species of *Oryza* and their origin and progenitors have been reviewed in detail by Chandraratna[10] and by Chang[11] and these authors may be consulted for further details. From India cultivated rice spread to Egypt, Europe, Africa, Australia and the Americas, and from China it spread to Korea and Japan.

VARIETIES OF RICE

Rice has been cultivated for thousands of years under widely different geographic and agroclimatic regions. During this long period a multitude of forms and varieties have evolved. Based primarily on geographic adaptation and morphological characters, the cultivated rice of the world can be broadly divided into three varietal groups, indica, japonica and javanica.[10 11 12 55] Some workers rank these groups as subspecies of *Oryza sativa*. The japonica group includes varieties from Japan, Korea, and northern China. Japonicas from Japan are adapted to temperate climates, however, some japonicas from Taiwan are adapted to the subtropical or warm temperate regions. The indicas include varieties from India, southern China, Taiwan, Ceylon, Java and other regions. Javanicas include a small number of varieties from Indonesia which are referred to as bulu varieties.

The distinguishing characteristics of the indica and japonica groups may be summarized as follows:[10 12]

Indicas	*Japonicas*
profuse tillering	moderate tillering
broad, light green leaves	narrow, deep green leaves
usually sensitive to photoperiod	often sensitive to photoperiod
have grain dormancy	do not have grain dormancy
rarely responsive to nitrogen fertilizer	responsive to nitrogen fertilizer
susceptible to shattering	resistant to shattering
slender, flat grains	short, roundish grains
typically awnless	awnless to long awned
thin and short hairs on glumes	dense and long hairs on glumes

In addition to the morphological physiological differences there is a large amount of hybrid sterility between the two groups of varieties [10]

The javanica varieties are more or less intermediate between the other two groups and are considered by some to be variants of the indica varieties [11] Plants of javanica are typically low tillering with broad, stiff, light green leaves, photoperiod insensitive, moderately responsive to nitrogen fertilization, and resistant to shattering They have broad, thick grains, are typically long awned, and have long hairs on the glume

Variety classifications in each group have been developed on the basis of grain size and other morphological and physiological differences [10 16] The aus varieties of India and Pakistan are photoperiod insensitive (flowering is unaffected by day length) and have a growing period of short duration like the japonicas, while the aman varieties are photoperiod sensitive (flower with short days) and have a growing period of long duration

Rice is grown in widely different regions, from deeply submerged areas to high altitudes The rice varieties adapted for growing in submerged areas with 1 to 2 metres of water are called *shallow water* varieties, while those with ability to withstand 3 to 5 metres of water are called *deep water* or *floating* varieties In deep water rice the stem elongates with the rising level of water thus keeping the plants floating The varieties adapted to high altitudes, normally referred to as *high altitude* varieties, have a growing period of short duration and will grow at lower temperatures than varieties commonly grown at lower altitudes Varieties grown on dry land are called *upland* varieties

Some rice workers believe that the japonica varieties of China and Japan and the javanica (bulu) varieties of Indonesia were derived from the aus types of India, while the tjereh varieties of Indonesia were derived from the aman types of India [11] Others consider japonica varieties to be hybrid derivatives from natural crosses between indica varieties and strains of Asian *Oryza perennis* which is prevalent in south China and Taiwan Another possibility is that the japonica varieties were derived from indicas which in turn originated from *O perennis* While discussing the varietal groups of rice it should be remembered that with current progress in rice breeding, varietal patterns are fast changing Many American varieties now have both indica and japonica genes in them and these are being introduced into the breeding programmes of southeast Asia Intervarietal crosses among indica and japonica varietal groups in the rice breeding programmes throughout the world are leading to increasingly more complex varietal patterns With these developments the distinctive characteristics by which the varietal groups were formerly identified are rapidly being merged in the new varieties and it will become difficult to identify many future varieties with these traditional varietal groups

BOTANY AND GENETICS OF RICE

The genus *Oryza* is a member of the grass family, *Gramineae* The rice inflorescence is a panicle which bears single-flowered spikelets (Fig 7 1) The rice flower differs from that of other cereals in having six stamens (Fig 7 2) The flower is surrounded by a lemma and palea, structures which form the hull or husk that encloses the threshed grain or paddy The outer glumes are usually obscure, being only about one fourth the length of the lemma and palea, although in some varieties they approach the lemma and palea in length The blooming of rice normally occurs between 8 and 11 A M [1 50 51] The flowers in a single panicle bloom over a period of seven to ten days, but most of the flowers bloom between two to four days after emergence of the panicle from the boot leaf The time and rate of blooming varies with the variety and with environmental factors such as temperature, humidity and light The breeder needs to observe when maximum blooming takes place under the conditions that he is growing rice in order to know when to make emasculations and when pollen can be most easily collected for crossing Pollen is generally shed at the time the flower opens Blooming of the spikelet starts at the apex of the panicle and proceeds downwards [1 50] The rice flower is normally self pollinated The extent of natural crossing varies from 0 to about 3 percent with an average of about 0 5 percent, [5 10 53] depending upon the variety, the season, and the environment

Crossing Techniques. Several methods have been used for emasculating rice flowers Before emasculation immature spikelets or those previously flowered are removed from the panicle keeping only flowers that will bloom the following day The conventional method, still used by some rice

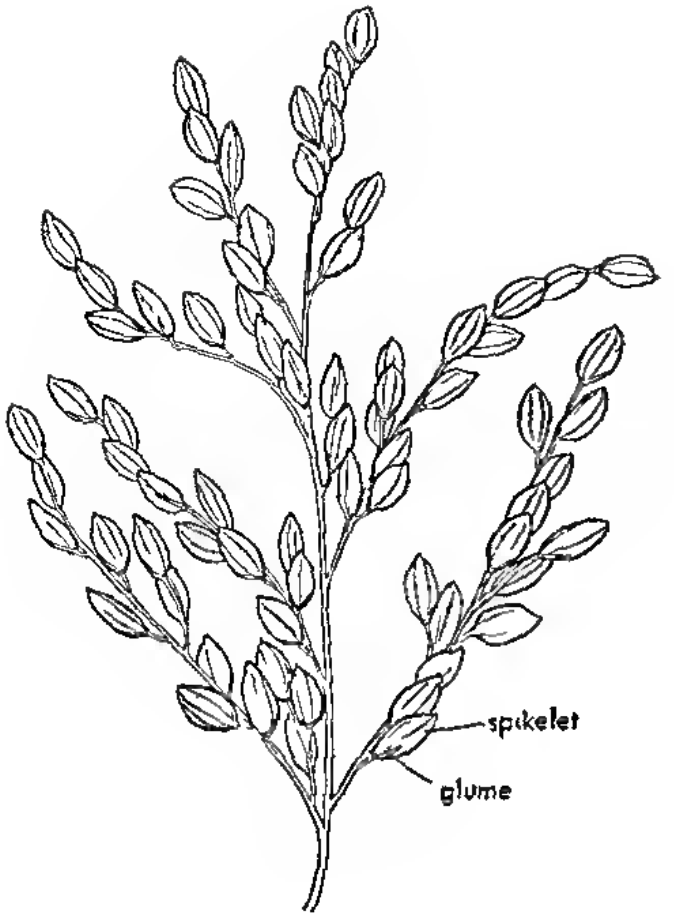


Fig 7 1 Portion of a panicle of rice The rice inflorescence bears single-flowered spikelets

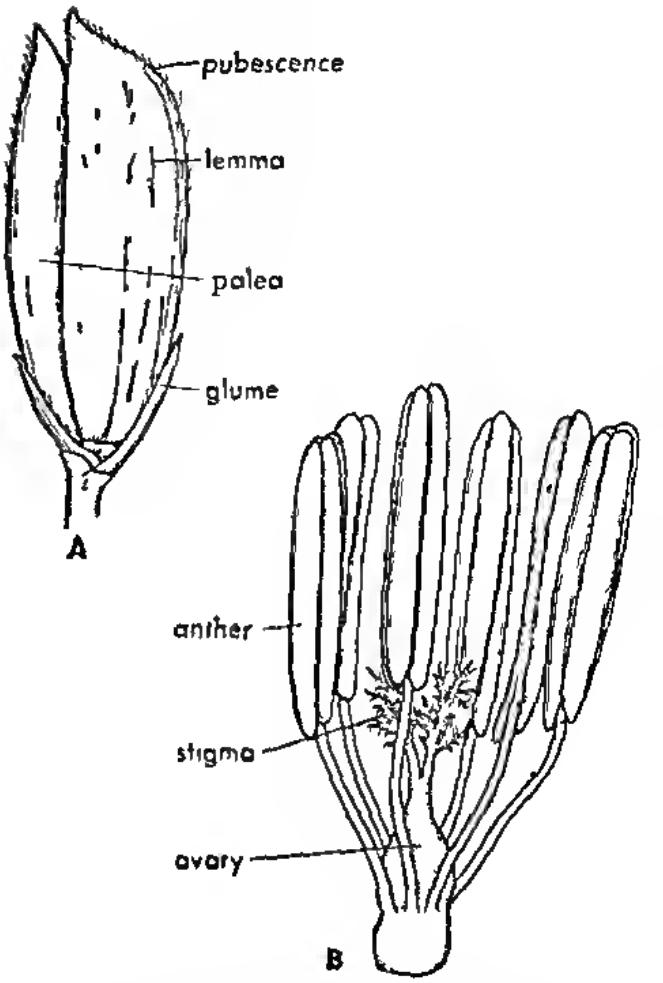


Fig 7 2 Spikelet and flower of rice A Spikelet of rice The lemma and palea form the hull that encloses the rice grain The glumes are small and inconspicuous B Flower of rice The rice flower differs from that of other cereals in having six stamens

breeders, is to separate the glumes with a pair of forceps, in the early morning about 1 to 2 hours before pollination, and remove the six stamens Emasculation and pollination may be facilitated, however, by cutting off the end of the florets in a manner similar to that used with other cereals such as wheat and barley [24 27 30] Clipping across the anthers just above the attachment of the filament will remove most of the anthers at the same time and expose the remnants of the anthers so that they can be removed with fine pointed tweezers (Fig 7 3)[24] Emasculations are done in the afternoon and pollinations the following morning After emasculation flowers are covered with a butter paper bag (Fig 7 4)

Hot water may be used to open the florets of rice before crossing In the hot water treatment the rice panicle is immersed in water contained in a thermos flask at 42 to 44 degrees Centigrade for a period of 5 to 10 minutes (Fig 7 5) [10 27] Panicles in the second or third day of blooming are chosen as female parents and spikelets that have already flowered and immature florets are removed An hour or so before blooming normally begins, the tiller is bent over carefully to avoid breaking and inserted into the hot water The thermos bottle may be supported on a troughlike holder at an angle of about 35 degrees to prevent loss of water This treatment causes the florets to open in a normal manner and the stamens may be removed without injury to the stigma Pollinations must be made within a 30 minute period before the glumes close naturally

Successful pollinations require mature and healthy anthers Florets nearing the blooming stage are opened, and the turgid anthers are taken with forceps and broken over the stigma Pollen may also be dusted over clipped florets by shaking a

Fig 73 Panicle of rice which was emasculated by clipping across the florets and removing portions of anthers remaining This panicle was later pollinated and seeds have developed in many of the florets

shedding panicle over them [24] Pollen of rice does not normally remain viable for more than a few minutes Seed set in rice is generally lower than with wheat or barley

Varieties to be used as parents in crosses or F_1's to be used as parents in backcrosses may be grown in pots and crossing done in small screen houses This gives better footing and increases the efficiency and convenience in making crosses (Fig 76)

Vegetative Propagation in Rice The rice plant starts tillering during the early vegetative phase The plant can be vegetatively propagated by separating the tillers and planting them as individual plants (Fig 77A and B) [56 59] The total number of plants that can be raised during a season from one seedling will depend upon the

Fig 74 Rice panicles are covered with glassine or butter paper bags following emasculation to protect them from pollination by foreign pollen

Fig 75 Hot water method of emasculation in use at the Central Rice Research Institute, Cuttack

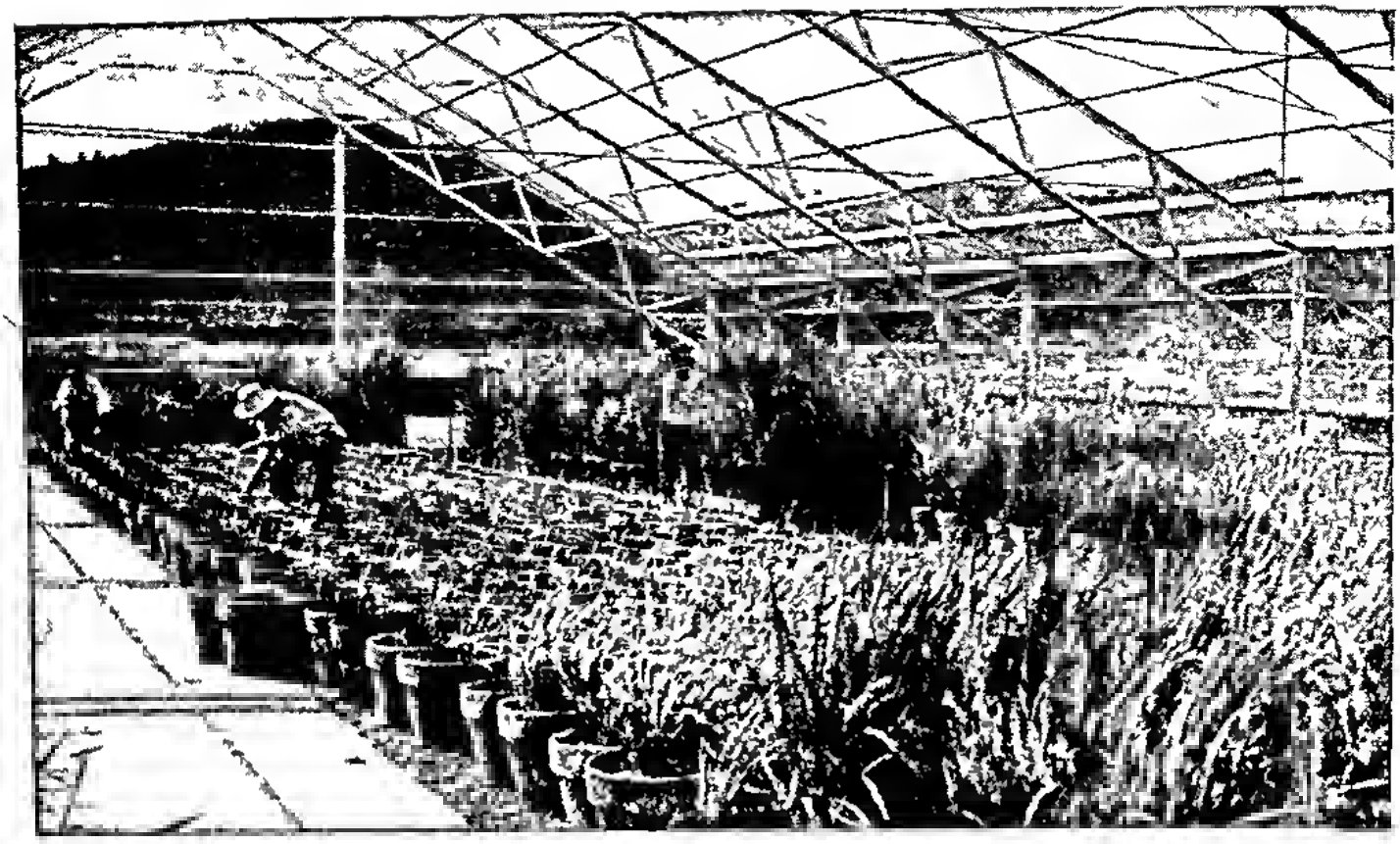
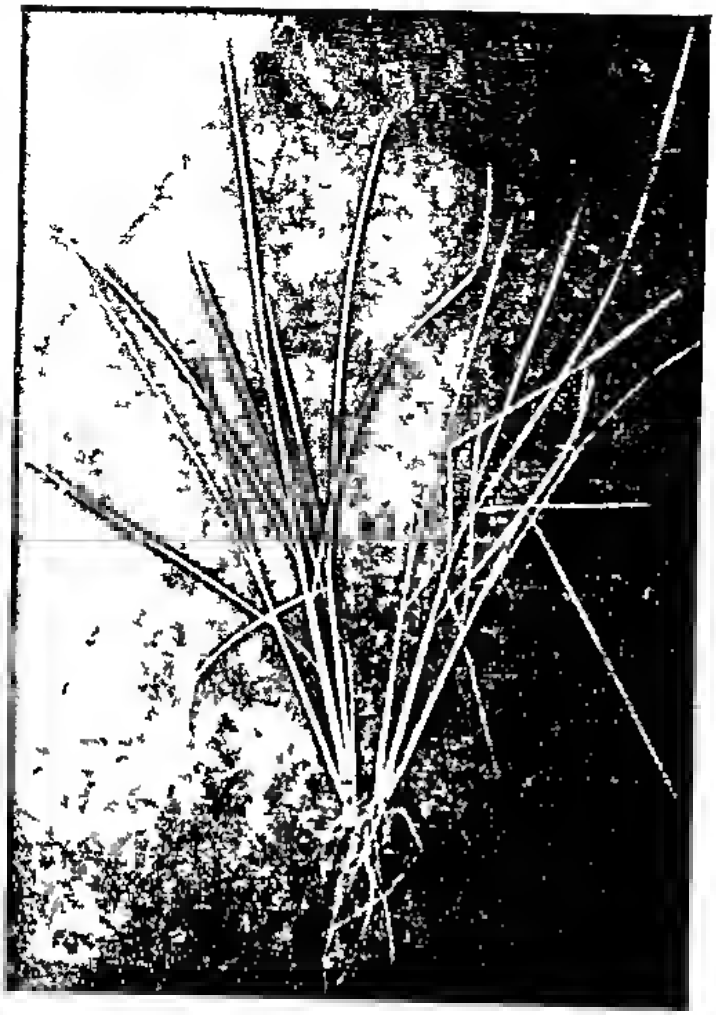


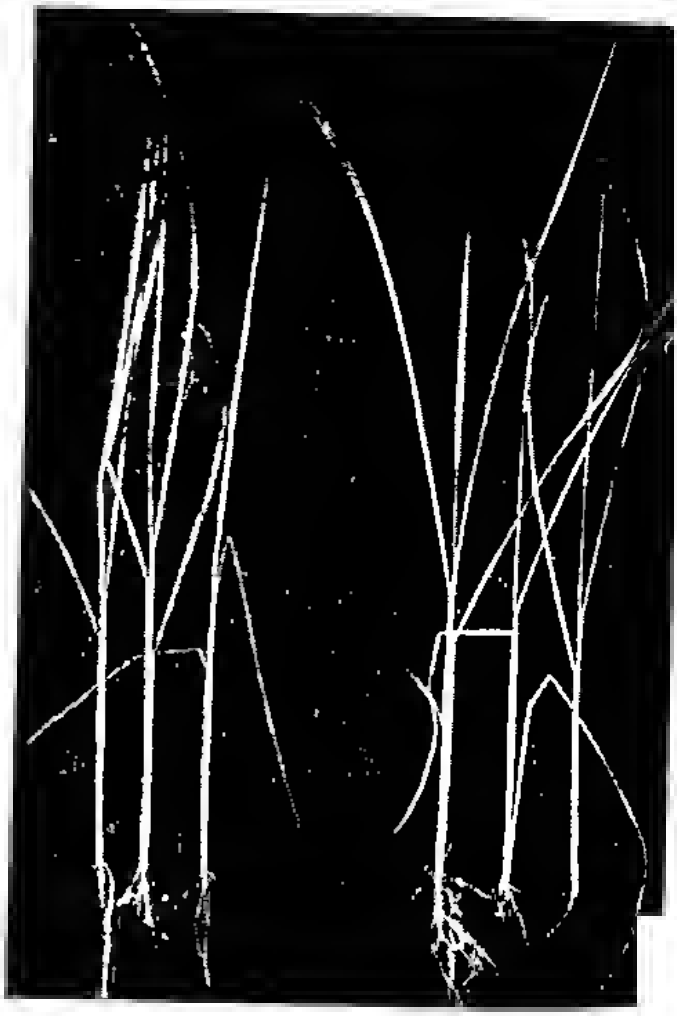
Fig 7 6 Screenhouse used at the International Rice Research Institute Los Banos Laguna the Philippines, for crossing rice varieties Labour required for crossing is utilized more efficiently here than when plants are growing in water in the field

tillering ability and the duration of growth of the variety With photoperiod sensitive and long growth duration varieties, the clones can be separated and multiplied 3 to 6 times as they have a longer vegeta tive growth period, but with photoperiod insensitive and short duration varieties only 2 to 3 multiplica tions will be possible Vegetative propagation can be utilized by the plant breeder to his advantage in several ways (*a*) If the seed set in crosses is low the number of F_1 plants can be increased in order to obtain a larger amount of F_2 seeds (*b*) A particular plant in a backcrossing programme may be retained until the genotype is proven in the next generation (*c*) Replication of single plants is possible (*d*) In sterile F_1 hybrids the plant can be propagated and maintained for a period of time to permit further study or for crossing (*e*) Photoperiod response of single plants can be determined by growing tillers separately in 10 hour and 16 hour photoperiods Vegetative propagation is also useful for the rapid increase and the maintenance of purity in breeders seed The latter aspect will be discussed in the chapter on Seed Production Practices

Genetic Studies. *Oryza sativa*, the cultivated rice, has a somatic chromosome number of $2n=24$ which corresponds to that of many of the wild species of *Oryza* Some wild species of *Oryza* are tetraploid with somatic chromosome number of $2n=48$ *Oryza sativa* behaves like and is usually considered to be a diploid species, but there is some genetical and cytological evidence to indicate that it is a secondary polyploid in nature and that the basic chromosome number is 5 [10 21 43] Observations on secondary association of chromosomes during meiosis and the presence of duplicate genes indicate *O sativa* to be an aneuploid species The 12 haploid chromosomes in this theory are *a*, *b*, *c*, *d*, *e*, *a'*, *b'*, *c'*, *d* , *e'*, *a"*, *b"*, (Fig 7 8) The hypothesis proposed to explain this chromosome relationship is that a species with a haploid set of five chromosomes (*a b c d e*) hybridized with a second species with a haploid set of five chromosomes (*a' b' c' d e'*) Through some meiotic irregularity two chromosomes (*a" b"*) were duplicated in the hybrid and this was followed by doubling of the chromosomes to produce the fertile progeny *O sativa* The wild



7 7A



7 7B

Fig 7 7 Vegetative propagation in rice A Two plants of rice which are in the correct stage of growth for vegetative propagation by tiller separation B Tillers which have been obtained by division of the plants in A Each tiller, upon transplanting, will produce a new plant

progenitors of *O sativa* with five chromosomes have not been found and may be extinct

Many inheritance studies have been made with rice in India, Japan, the United States and other countries These have been reviewed and summarized by several rice investigators [10 11 29 41 42 54 61] Most of the inheritance studies with rice have dealt with simple morphological characters and colour markings, many of which are relatively unimportant to the breeder However, the number of inheritance studies dealing with vital physiological and pathological characteristics, such as height, tillering, lodging resistance, quality, disease resistance, or other characters of economic importance, are increasing

Until recently the genome designations and systems of gene nomenclature in rice were varied and confusing [11 31 32 35 54 55] At an "International Symposium on Rice Genetics and Cytogenetics" sponsored by the International Rice Research Institute, Los Baños, Philippines, in 1963, a uniform genome designation for rice was recommended [11,33 5] A uniform system of gene symbols was also recommended by the International Rice Commission of the Food and Agricultural Organization of the United Nations [11,19] About fifty genes have been identified and assigned to the 12 linkage groups, but data are inadequate for a complete mapping [11] The genome of *Oryza sativa* is designated *AA*

Many interesting genetic and cytogenetic studies are being made with rice in attempts to develop a genetic basis for species relationships [35 45 63 73] Interspecific crosses in rice are generally accompanied by a high degree of partial or even complete

Fig 7 8 Diagrammatic representation of haploid chromosome set from *Oryza sativa* It is presumed that *a b c d e* originated from one species and *a , b , c , d e* originated from a second species Through some meiotic irregularity two chromosomes were duplicated giving rise to *a" b"*

sterility in the hybrids The degree of sterility in the F_1 is determined by the lack of affinity of the parents There is also a rather regular occurrence of partial sterility in wide intervarietal crosses within the *O sativa* species This is frequently observed in the japonica x indica crosses Explanations have been offered for this phenomenon on the basis of (*a*) recombination and segregation of specific genes (genetic), (*b*) chromosome abnormalities and irregularities (chromosomal), and (*c*) cytoplasmic influences [10 11 18] In general, however, this has not formed an obstacle to breeding since fully fertile lines with the full range of recombinations of desirable traits can usually be picked up in segregating generations of intervarietal crosses between distantly related plants if rigorous selection is practiced

Genetic male sterility in rice has been identified by several research workers [10] All were inherited as single gene recessives Genetic male sterility could be a useful tool in a rice crossing or back crossing programme to eliminate emasculation A genetic male sterile form inherited as a single gene recessive character may be introduced into another variety or maintained by a backcrossing programme, the progeny segregating in a ratio of 1 fertile 1 male sterile Cytoplasmic male sterility in rice, if available, might prove useful for development of hybrid rice on a commercial basis

Mutations have been common in rice, and these may help explain the origin of the large number of varieties grown throughout south and southeast Asia [12] Colchicine induced tetraploids have been produced, but the polyploid forms generally tiller less and are less fertile than the corresponding diploids Autoploidy does not appear to have immediate practical value to the breeder, except for the induction of polyploidy in connection with interspecies hybridization

Further information on genetics of rice will be discussed in connection with specific breeding objectives Varietal and interspecific crossing will be discussed further under the hybridization method of breeding

Central Rice Research Institute. The Central Rice Research Institute, Cuttack, India, was established by the Government of India in 1946 to conduct fundamental research on an All India basis in all aspects of rice production, breeding, genetics, diseases and insect problems This institute maintains a large world collection of wild and cultivated rices Intensive studies are being made on the taxonomy and cytology of the species of *Oryza*, japonica x indica crosses, vegetative propagation, blast resistance, and other problems

All-India Coordinated Rice Improvement Project. An All India Coordinated Rice Improvement Project was organized in 1965 to coordinate the breeding and other researches on rice conducted by state and central governmental organizations in India. The Rockefeller Foundation in India is cooperating in this coordinated effort to accelerate the rice breeding programmes [illegible] by sharing of information and breeding [illegible]ng various states Uniform [illegible]s

grown throughout India as a part of this co-operative programme

International Riee Research Institute. The International Rice Research Institute was estab lished on the campus of the College of Agriculture of the University of the Philippines, Los Baños, in 1962, through the joint efforts of the Rockefeller and Ford Foundations A vigorous plant breeding programme has been initiated in an effort to develop high yielding, photoperiod insensitive strains that may be utilized either directly or as parent materials in other rice breeding programmes throughout southeast Asia Genetic studies on rice as well as research on disease and insect resistance, physiology of rice, chemistry, agronomy and related fields are being conducted A large world collection of tropical and subtropical rice varieties and strains is being maintained

METHODS OF BREEDING RICE

Methods of breeding rice are comparable to those used with wheat These were discussed in the previous chapter They are introduction and germ plasm collection, selection, and hybridization Mutation breeding and polyploidy may be used for specific purposes

Introduction and Germ Plasm Collection. Introduction of exotic types has not played an important role in the breeding of rice varieties in southeastern Asia in the past In countries like India, Burma, Ceylon and Pakistan, there has been a multiplicity of varieties grown since early times Breeding in rice in these countries has been largely devoted to improvement of the native varieties and to development of locally adapted types While varieties have been introduced from China, Japan, the U S A , and other countries, generally, they have not been found to be well adapted and have seldom been used for direct cultivation Recently, several varieties with short stature, photoperiod insensitivity, nitrogen responsiveness short growth duration, and high yield potential have been introduced from Taiwan to India, the Philippines, and other countries in southeast Asia Several of these varieties, particularly Taichung Native 1, an indica type, is being tried on a large scale in all of the states in India While it is too early to assess the extent to which these varieties will be grown directly, they are being used exten sively in breeding programmes to combine short stature, nitrogen responsiveness, and photoperiod insensitivity with disease resistance and adaptation of Indian varieties They, or similar types being developed at the International Rice Research Institute, Los Baños, will surely have an important influence on the Indian varieties in the future as well as those of other countries in south and south east Asia Limited utilization of japonica varieties from Japan has been found in some areas of India and Burma at high altitudes

One of the important requirements in plant breeding is to have available large germ plasm collections to serve as a storehouse of genes to which the plant breeder may have access Throughout tropical Asia many local strains are grown which by selection, both natural and artificial, have become over many centuries adapted to the varying climatic conditions in which rice is grown in this vast geographic area It is important that re presentative samples of as many of these types and varieties of rice as possible be maintained for use in future breeding programmes In India, a rice collection of about several thousand varieties is being maintained at the Central Riee Research Institute, Cuttack Many of these varieties were collected in India and adjaeent countries in south and southeastern Asia A eollection of about 10 000 strains collected from all over the world is being maintained at the International Riee Research Institute, Los Banos, Philippines A large eollection is also maintained by the United States Department of Agriculture in the U S A

Selection. Unimproved varieties of self pollina ted crops will generally be mixtures of pure lines After cultivation for a long period of years a variety, due to natural crossing, mutation, and other causes, becomes a mixture of many homozygous genotypes Improvement in these varieties by selection may be made either by mass selection, in which a group of the constituent genotypes are bulked together, or by pure line selection, in which a single genotype is isolated and increased These selection procedures were described in the chapter on Methods of Plant Breeding and examples were cited in the chapter on Breeding Wheat, a crop which like rice is self pollinated

With the multitude of local forms of rice grown all over tropical Asia it was logical that selection, both mass and pure line, would be used in the early years to purify the mixtures and to isolate superior

genotypes which could be developed into new varieties Since many varieties of rice now in cultivation are improved varieties and have arisen by selection from local or hybrid populations, selection within them is not generally a fruitful method of breeding Only by the isolation of a chance mutant with superior characteristics, or by the selection of a superior segregate from a natural hybrid, could an improved type usually be obtained

Hybridization Hybridization provides the means for developing new populations from which, as a result of segregation and recombination, new genotypes may be selected In India, hybridization as a method of breeding rice was started in the early part of this century and many varieties have been released from this breeding procedure

Selection of suitable parents is an important step in hybridization, and the success of a crossing programme will depend primarily on this choice Choice of parents is guided by the objectives the breeder has in mind It is interesting to see how the selection of the parents changes with shifting of objectives in breeding In the early years in India the use of chemical fertilizers was inconceivable as they were never available Green manure and farm yard manure, which were also very limited, were the main sources of fertilizer, and the rice straw was needed for cattle food Hence, tall and high tillering parents were included in most crosses Little attention was given to lodging resistance As human population increased and their needs began to overtake food supplies, more consideration was given to the utilization of chemical fertilizers, although still at a relatively low level because rice varieties in use lodged when fertilizer was applied To improve the varieties in this respect and to improve their response to chemical fertilization, a coordinated japonica x indica hybridization project was initiated in India and other Asian countries [41 58] More recently, scientists at the International Rice Research Institute have stressed the importance of plant types that will stand without lodging and respond to levels of fertility far higher than fertility levels formerly visualized for rice Also, varieties are being planned with short growth duration and photoperiod insensitivity, so that they may be planted in different seasons and at different latitudes This latter concept has led to utilization of Taichung Native 1 from Taiwan, and similar types, as parent varieties in large numbers of crosses These developments indicate the need for the breeder to have clear and well defined objectives before choosing the parents in a cross

After the crosses have been made the segregating populations may be grown and either the bulk population or the pedigree method of selection may be used, depending upon the particular cross and the facilities available These methods were described in detail in the chapter on breeding methods In breeding rice for short stature and plant type associated with nitrogen responsiveness, the pedigree selection procedure is particularly appropriate since desirable plants can be recognized easily at an early generation [23] In crosses between the tall, leafy, tropical indica varieties and the shorter, low tillering, nitrogen responsive varieties, either japonica or indica, the latter types are poor competitors in mixtures with the tropical indica types and are rapidly eliminated from bulk populations by natural selection [23] An alternative procedure is to remove the tropical indica types from the F_2 population and select from the remaining short stature types The tall and short stature types may be identified in the nursery or in the field

Intervarietal crosses have been used almost exclusively in the development of varieties by hybridization thus far Interspecific crosses have been used mainly to study the nature of hybrid sterility, the interrelationships of species, and for genome analysis The greatest obstacle to interspecific hybridization is the high sterility in the hybrids Due to the difficulties of obtaining fertile hybrids, and considering that suitable sources of resistance genes are available within the *O sativa* species, it appears at present that exploitation of intervarietal hybridization is much more practical and easier to accomplish than interspecific hybridization The wide range of genetic variability within the *O sativa* species is assurance that the limits of recombination are still very great

The backcross procedure may be used to add genes for specific characteristics to an acceptable local variety, or may be used to concentrate genes for a polygenic character The backcross procedure in breeding was outlined in Chapter 4 and its use in breeding wheat was discussed in the preceding chapter With rice, when a suitable plant type has been established, the backcross method is

effective in introducing easily transferred traits like maturity, disease resistance grain dormancy, glabrous glumes shattering resistance, endosperm characteristics and others At the International Rice Research Institute the short stature required for development of fertilizer responsive varieties and other characters with simple inheritance are being added to many local and tropical varieties Short stature in Taichung Native 1 is conditioned by a single recessive gene With wide crosses a single backcross is often made to the variety with the most desirable plant type

Hybrid vigour in F_1 generation plants has been noted by many workers in such characters as height tillering ability earliness and yield [54] Utilization of hybrid vigour for the commercial production of hybrid rice as is being done in wheat, is dependent upon availability of suitable cytoplasmic male sterility and restorer genes or other means for controlling pollination on a mass production scale Also seed set with cross pollination must be sufficient to make seed production economically sound

Mutation Breeding The first x ray induced mutation in rice was reported from Japan in 1934 [11] In India the first report of induced mutation was made by Ramiah and Parthasarathy in 1936 [53] Since then a large number of studies have been made on induced mutations in rice and the results of mutation breeding have been reviewed in detail by several workers [10 11 44 54] Although many of the characters originating by mutations like chlorophyll deficiencies are not of economic importance yet various mutations affecting grain characteristics quality plant height maturity, disease resistance and other characters have been observed In India a mutant strain which has shorter and stiffer straw than the parent variety T 141 but otherwise is similar to it has been selected following x ray treatment of T 141 at the Orissa University of Agriculture and Technology (Fig 7 9)

Polyploidy Both natural and induced polyploidy has been studied in rice [10 11] Although the tetraploids usually have *gigas* plant characters their reduced vigour and seed fertility limit their economic use Polyploidy may be useful as a tool to achieve fertility in interspecific crosses with rice

OBJECTIVES IN BREEDING RICE

The principal objectives in breeding rice are

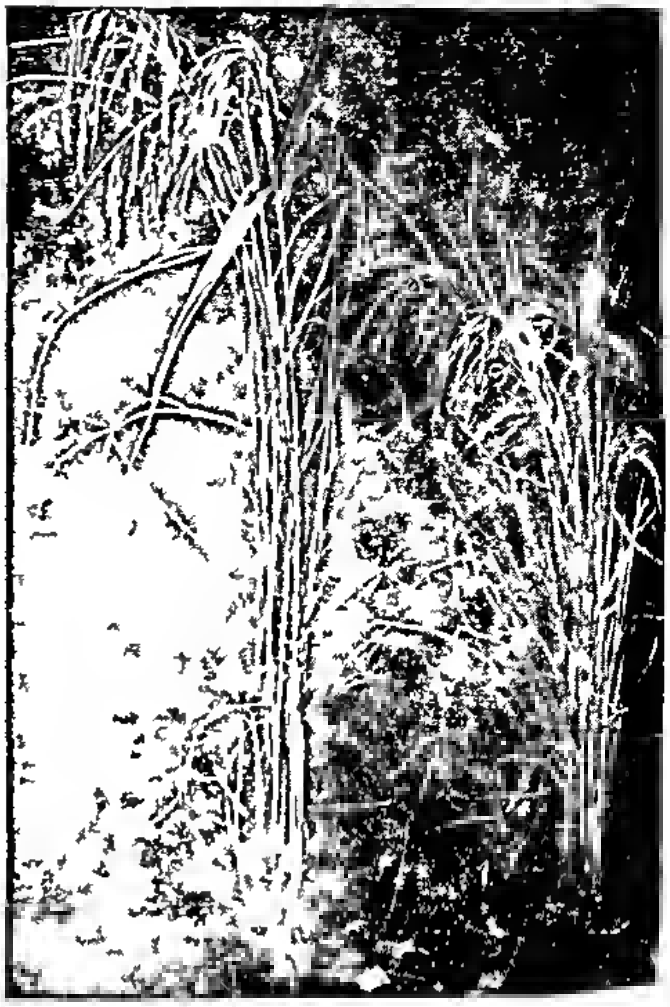


Fig 7 9 X ray induced mutation in rice The short selection at right was made following the irradiation by x rays of seed of the rice variety T 141 The short mutation is otherwise similar to the T 141 variety

yield maturity resistance to lodging and shattering disease resistance insect resistance quality and adaptation for specific environments or uses

Yield Rice is a crop with a high yield potential Yet, the average yield of existing varieties of rice in the whole of tropical southeast Asia is one of the lowest in the world The breeder in this area thus cannot overlook the possibility of obtaining genetic combinations with much greater yield potential than those available in the varieties now under cultivation Yield is a complex character which may be influenced by many physiologic processes within the plant It is also affected by the response of the genotype to the environmental factors in which the plant is grown In addition to assembling into a variety the most desirable combination of genes affecting the plant's capacity to manufacture

food materials and to store them in the grain, it is necessary to include genes for resistance to those conditions in the environment which unfavourably affect the yield, such as lodging resistance, disease resistance, insect resistance, and others To reach this objective considerable attention is being given in the breeding of rice for specific plant types and for responsiveness to fertilizers These will be discussed

A PLANT TYPE The relation of the plant type to yielding ability has been studied extensively in Japan [37 40 67 68 69 70] The far reaching implications of these studies have been recognized at the International Rice Research Institute through comparisons of the plant characteristics of the high yielding varieties of the world, both japonicas and indicas, with plant characteristics of the low yielding indica varieties of tropical southeast Asia [22] These studies convincingly show that high yield potentiality in a variety is related to specific morphological characteristics which characterize the plant type

Plant characteristics which are associated with high yield potential are (*a*) nitrogen responsiveness as indicated by grain yielding capacity, (*b*) short stature, thick stiff culms, and compact panicles that hold the plant erect without lodging even with high applications of nitrogen fertilizers (*c*) short, narrow, thick, and dark green leaves that stand upright and thereby utilize light efficiently, reduce shading, and remain functional until the grain is nearly mature (*d*) seedling vigour, early tillering and early maturity, (*e*) photoperiod insensitivity so that planting date will be independent of seasonal limitation or latitude, and (*f*) floret fertility even at high nitrogen levels [7 22 23] This plant type marks a critical departure from the tall, high tillering, weak strawed, long duration, leafy types which have predominated in south and southeastern Asia for a thousand years (Fig 7 10) The upper leaves of this latter type shade the lower leaves which then die prematurely and cannot contribute to final grain production Plants of the type outlined above will have high potential for yield because they have high photosynthetic efficiency, make the maximum utilization of light by the erect leaf position which permits penetration of light to the lower leaves and reduces mutual shading, have reduced respiration, better standing ability and maximum response to fertilizer This knowledge of

Fig 7 10 Comparison of plant types in rice Left Short, erect leaf dark green, nitrogen responsive varieties Taichung Native 1 and Chianung Right Tall leafy high tillering indica varieties BJ 1 and MTU 15 The short erect varieties are being used extensively at the International Rice Research Institute in rice breeding programmes for southeast Asia

plant type is resulting in many rice breeders of southeast Asia orienting their breeding toward utilization of similar plant types as a means for improving yield Sources of the plant characters needed for development of suitable plant types are found in japonica varieties, in short stature indica varieties such as Taichung Native 1 and I R 8, in U S A varieties, and in Surinam varieties

If American or Surinam varieties are used in crosses, selection for higher tillering may need to be practiced American varieties have been developed for direct seeding and are low tillering Under transplanting with wide spacing the tiller number may be too low to give maximum yield

B NITROGEN RESPONSIVENESS High nitrogen fertilization is essential for increasing productiveness of the rice crop Most of the rice varieties now grown in southeast Asia do not respond to increasing levels of nitrogen fertilization and the nitrogen response curve generally declines after applications of 30 to 40 kilograms per hectare have been reached Further increases in the doses of nitrogen result in lodging of the plants thus leading to further reduction in yield

Nitrogen responsiveness is primarily a varietal characteristic which cannot be disassociated with the plant type [66] The response to nitrogen varies

with the season,[66] cultural management, and time of application of the nitrogen [9] The varietal difference in response to nitrogen is reflected in the efficiency of dry matter production and its distribution between grain and straw [39] Low nitrogen responsive varieties grow vigorously under heavy fertilization in the early stages of growth producing large numbers of tillers and long broad leaves This heavy growth results in excessive shading thus bringing about an adverse balance between photosynthesis and respiration which leads ultimately to weak reproductive growth [65] High nitrogen responsive varieties produce small leaves that remain green until maturity, reduce mutual shading, and remain photosynthetically efficient over a longer period [71] Earliness in maturity, moderate tillering ability, and insensitivity to photoperiod are also associated with high nitrogen responsive types [23] Nitrogen responsiveness is found both in varieties with high panicle number and with high panicle weight [66] Earliness in time of heading, with a long period for grain development and maturation, is considered to be desirable [71] Responsiveness to high fertilization is, in reality, associated with various physiological processes related to uptake and assimilation of nitrogen, translocation and storage of food products, and activity of roots, as well as resistance to lodging and disease [38] Floret sterility increases with heavy fertilization in the low responsive types [23] The morphological characteristics of the plant responsive to fertilizer are essentially the same as described above for a high yielding plant type and for lodging resistance The difference is mainly in their physiological activity

Genetic sources of responsiveness to nitrogen are available in both japonica and indica types The SML varieties of Surinam, indica varieties of Taiwan like Taichung Native 1 and I geo-tze, some japonica x indica lines from the southern U S A , and ponlai (japonica) varieties of Taiwan are all suitable sources [23]

The best procedure for screening breeding materials for responsiveness to nitrogen is to grow the segregating populations with high fertility levels and to select for early maturity, suitable plant type, and low floret sterility Coincident with the increased yielding ability, it will be necessary to improve the ability of the rice plant to hold up a heavier yield of grain without lodging Other deterrents to higher yield are susceptibility to diseases and pests Each of these objectives must be considered in the breeding of higher-yielding varieties

Early Maturity. Rice varieties may be classified *early*, *medium*, or *late*, according to the length of time required by them to reach maturity In the past it has been the general belief that late maturity types are higher in yield than early maturity types The duration of late maturing varieties is from 150 to more than 200 days while duration of early varieties is from 80 to about 140 days Recent studies have shown that early varieties with the plant type described in the preceding discussion maturing in about 110 to 130 days, have equal or even higher yielding ability than the late maturing varieties In addition, early varieties permit growing of two or more crops successively on the same land and helps to escape pest or disease infestation and vagaries of nature like flood and drought Moreover the cultivator has to attend to the crop for a lesser number of days in comparison to late types, and utilizes less irrigation water in irrigated crops Hence, the recent trend in breeding rice is toward the development of earlier maturing varieties

An important factor associated with maturity is the photoperiod sensitivity of the plant The long duration aman varieties of India and Pakistan are photoperiod sensitive, responsive to short day, and hence are seasonbound with respect to maturity They are unsatisfactory for growing in the short days of winter If early varieties are to be developed so that successive crops of rice can be grown within the year, then the varieties must also be bred for photoperiod insensitivity

Sources for earliness and photoperiod insensitivity are available in japonica varieties and in many of the indica varieties, including the aus varieties Some have been listed in the discussion on breeding for plant type Some of these varieties also have the ability to become established and tiller quickly, a desirable characteristic in the tropics where water supply, weed control and other cultural practices are poor

There are many conflicting reports regarding the inheritance of early maturity in rice [10 11 54] Maturity in rice in many crosses is inherited as a relatively simple dominant character In other crosses lateness has been reported dominant In still other crosses maturity was reported to be determined

by multiple factors Duration of growth is affected by the physiological development of the plant and is complicated by response to photoperiod and to temperature The breeder will need to study the specific varieties he is working with and their response in the particular environment where he is working Early maturity in the short, fertilizer responsive, photoperiod insensitive varieties, now being used in many breeding programmes in southeast Asia, has a high heritability, is fixed quickly in segregating material, and is easily identified [23] In the cross Peta x I-geo tze, early maturity was inherited by two or more genes [13]

Resistance to Lodging and Shattering. Lodging in rice results in lower yields owing to inability of the lodged grain to fill normally, increased disease damage in the lodged grain, and losses in harvesting The loss in yield is related to the time and the amount of lodging Up to 75 percent loss was reported when plants lodge before harvesting [26] Lodging also results in a reduction in milling quality as a result of chalkiness in the kernel Short strawed varieties usually are less likely to fall than tall varieties (Fig 7 11 A and B) Resistance to root and stem rotting contribute to lodging resistance Lodging is also affected by environmental factors such as wind, rainfall, level of nitrogen and plant spacing

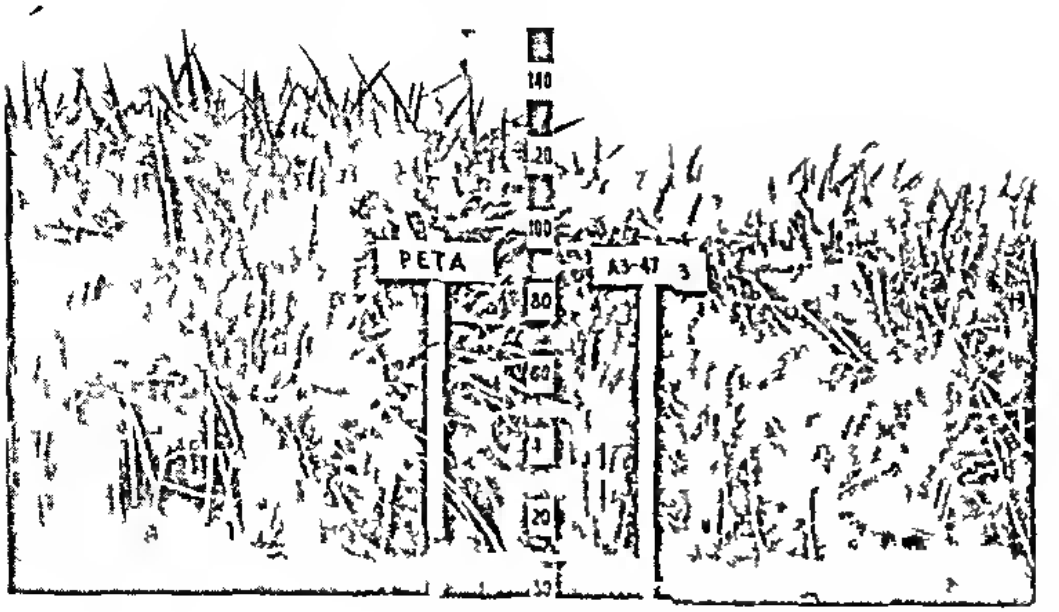
The indica rice varieties of south and southeast Asia are of long duration, tall, and weak strawed With these varieties lodging of rice before harvest has been accepted as inevitable by the cultivator, and the breeder in the past has done little to improve the situation Nitrogen fertilizer applied to the rice fields simply resulted in lodging occurring at an earlier date Current and future efforts in India and other countries in south and southeast Asia to increase the rice yield by increased fertilization will not fully succeed until adapted varieties of rice responsive to nitrogen fertilization and resistant to lodging are available to the cultivator

High yielding and nitrogen responsive varieties cannot be developed without resistance to lodging [26] Plant characteristics conferring lodging resistance include short stature, thick strong culms, short internodes at the base of the culm, leaf sheaths tightly wrapped about the base of the culm, erect leaves which permit light penetration, and a strong root system [12] Other requirements associated with these anatomical features are short duration, ability of leaves to remain green and productive, and ability of sunlight to reach the lower leaves and stems of the plant

The japonica varieties in general are more lodging resistant than the indica varieties, but some indica varieties, like Taichung Native 1 and I R 8, and varieties from the U S A, have the plant features described above and are lodging resistant and responsive to nitrogen fertilization Inheritance of lodging resistance is quite complex [11 13] However, inheritance of short stature is relatively simple In crosses with Taichung Native 1 and I geo tze, short stature is inherited as a simple recessive gene which shortens internodes and leaves [13] The gene for short stature does not have any apparent pleiotropic effects on grain size and sterility as is sometimes common with dwarfing genes Neither are there any apparent undesirable linkages with other needed traits such as seed dormancy, photoperiod response, maturity, disease resistance or cooking quality Unlike many dwarfs, these short stature rice varieties have a very high yield potential

Selection for lodging resistance may be facilitated by application of high levels of nitrogen fertilizer to induce lodging One of the dangers is that all of the breeding materials may become lodged and differences cannot be observed Lodging resistance is usually compared on a relative basis by expressing lodging as a percentage or on a scale of 1 to 10 Observations on lodging should be made at several intervals between panicle emergence and ripening, and the stage of development that lodging occurs should be considered, as well as the total lodging at maturity, in the evaluation of varieties

Losses of grain also occur from shattering In threshing rice, the grain should separate easily from the panicle, but it should not be so loosely attached that it will be shattered off and lost from wind or in handling Varieties differ in this characteristic The ease of threshing is determined by the attachment of the grain to the panicle, which in turn is influenced by the time of formation and nature of the abscission layer [34] The wild rices are extremely susceptible to shattering Usually each grain of wild rice is shed as soon as it is physiologically mature, because of the early formation of an abscission layer. In a few forms of [illegible] rice no abscission layer [illegible] these [illegible] difficult kinds to [illegible]



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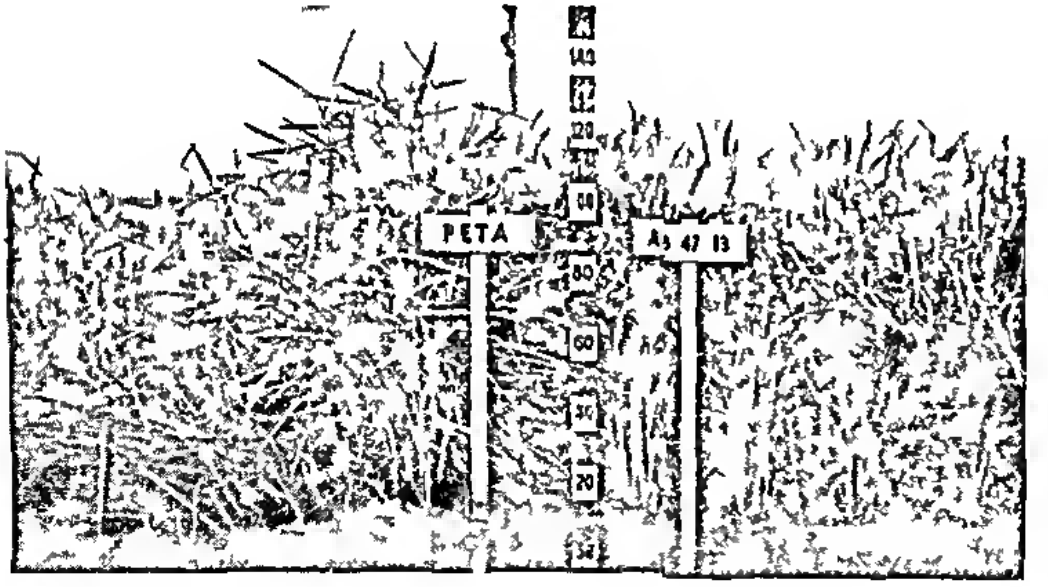


7 11B

Fg 7 11 Comparison of lodgng resistance A A tall leafy ndi a var ety Pe a growing adjacent to a short lodgng resistant strain B The Peta var ety has lodged n this pho o taken a short time la er wh le the lodgng resist ant var ety s still *standing*

varieties shatter less than ind ca variet es Moder ately firm threshab lity to give proper balance between ease of threshing and res stance to shatter ing should be given cons deration in the breeding of a rice variety This will be influenced by the method of threshing to be used whether by hand or by machine

Disease Resistance The princ ples of breeding for disease res stance in r ce do not d ffer from those that apply to the breed ng for resistance to disease in wheat Res stant var et es must first be found and then genes for res stance may be transferred to adapted variet es Some of the principal rice diseases that have received attention by rice breeders in south and southeast As a and breeding problems important in each will be d scussed briefly

A BLAST (*P ricularia oryzae* Cavara) Blast is the most serious fungus disease of rice in southeast Asia It is almost un versally present and causes damage in most rice growing areas Under favourable condit ons for disease development the rice crop may be almost completely destroyed

Spores of the rice blast d sease are airborne

They produce lesions on the leaves which may quickly expand, blighting the entire leaf or even the entire plant On more mature plants, the fungus may attack the neck, blighting the head, or causing it to be broken over The name 'rotten neck" is applied to this condition The fungus may also attack the nodes of the stem, causing them to turn dark and part of the stem above the point of attack to be killed Development of the blast disease is favoured by wet cloudy weather, high plant populations, high fertility (especially use of nitrogen fertilizers), and growing susceptible varieties [20] The incidence of the blast disease appears to be increasing in many countries, particularly with an increase in the use of nitrogen fertilizers In the past development of the blast disease was probably held down by use of relatively resistant native varieties at low levels of soil fertility

Breeding blast resistant varieties is now an important objective in rice breeding programmes in Japan U S A, India, Taiwan, the Philippines, and other countries,[7 21 37 57] and resistant varieties have been identified in each of the countries The problem of breeding for resistance is complicated by the large number of physiological races of the fungus [21] Furthermore, the races of the blast fungus appear to be different in different countries Varieties resistant in India may not be resistant in Taiwan or the Philippines Varieties resistant in the U S A may not be resistant in India or Japan If new races of the fungus develop from time to time, resistant varieties may become susceptible within a few years Comparisons of races present in different countries have been difficult because different differential varieties have been used in the different countries for identification of the races Currently, attempts are being made to develop a set of differential varieties which may be used uniformly in all countries as has been done with the wheat rust diseases A uniform system of identifying races would facilitate exchange of breeding materials among countries as well as identifying sources of resistance to the blast fungus The potential resistance of a variety in a particular country could be predicted if knowledge of the races present in the country and the reaction of the variety to the races were known

Extensive screening of varieties for blast resistance has been conducted in the world collections of varieties at the International Rice Research Institute, Los Baños, the Philippines,[20] the Central Rice Research Institute, Cuttack, India,[49] as well as in the U S A, Japan, and other countries The technique of screening under natural infection consists of growing seedling plants of the strains or varieties in short rows, with heavy nitrogen fertilization but without irrigation A susceptible variety is planted at regular intervals within the nursery, and in a border surrounding the entire nursery, to help build up inoculum (Figs 7 12 and 7 13) Mulching to keep the soil moist and watering in late afternoon to increase the humidity at night and dew formation on the leaves favours incidence and spread of the disease Ordinarily, airborne spores are sufficient to start infection, but natural infection may be supplemented by cutting infected leaves of rice into small pieces and spreading between the rows in the blast nursery Testing for resistance to individual races is done by growing plants in pots in a glasshouse and spraying the plants with inoculum of a specific race [34] Resistance to neck rot infection may be tested by injecting a spore suspension of the blast fungus into an emerging panicle [20] The testing of varieties for resistance has been aided by an International Uniform Blast Nursery Programme initiated by F A O in 1961[48] and now handled by the International Rice Research Institute [20] The programme also aids in determining race patterns of the fungus in different countries and in identifying varieties potentially useful as international differentials for race identification

Resistance in various studies has been reported to be controlled by one, two or three genes[11] with resistance partially dominant [20] Strains resistant in the seedling stage are also resistant to the same races of the blast fungus in the neck rot stage [48] Accession 6741 (CP231 x HO 12), accession 9914 (Mo R-500 x Nato), and H 105 from the U S A, Taichung 172 and 176, and Chinan 8 from Taiwan, and Kataktara from Pakistan are among the varieties resistant to blast at the International Rice Research Institute

B BACTERIAL LEAF BLIGHT (*Xanthomonas oryza*) Bacterial leaf blight is one of the most destructive rice diseases in India, Indonesia, the Philippines and other countries of south and southeast Asia. Bacterial leaf blight, called "kresek" in Indonesia, is characterized by appearance of pale greenish or white lesions on the leaf margins, yellowing or

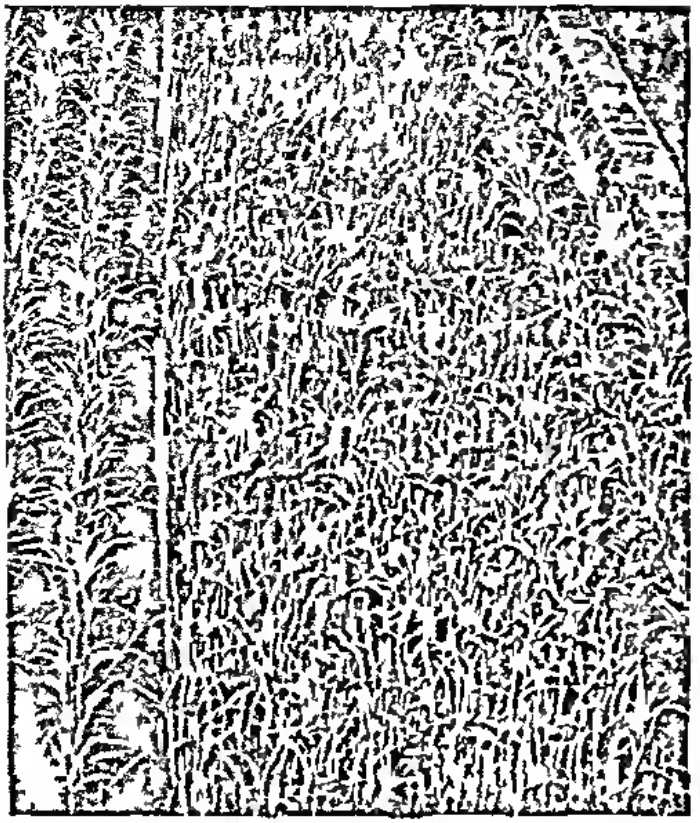


Fig 7 12 Screening varieties of rice for resistance to blast disease The varieties are planted in a bed in short rows with a susceptible variety planted in border rows

Fig 7 13 Comparison of susceptible and resistance strains in the blast resistance nursery The resistant strains are shown at left and at right The susceptible strains in the centre have been severely injured or killed by the blast disease

browning of the leaves and wilting of the plants Entire seedlings may be killed Breeding resistant varieties appears to be the principal means of control Screening tests at the International Rice Research Institute showed one variety of rice from the U S A and 13 from Taiwan to be resistant out of 102 varieties tested [20] Thirty varieties from 8 countries were rated intermediate in resistance Resistance was reported in many of the wild species of rice A high correlation has been observed in results obtained from inoculations made at the seedling stage and on the flag leaves at the flowering stage Inoculations are made by puncturing the leaves with needles covered with inoculum Accessions 6973 and 9797, Sigadis, Kaohsiung 68 Chianan 8 and Taichung 172 and 176 are among the resistant varieties A single dominant gene *Xe* is reported to control resistance to the disease.[11]

c VIRUS DISEASES As late as 1961, when the International Rice Research Institute was established in the Philippines, it was believed that virus diseases were unimportant in rice in southeast Asia [20] Since then at least 4 virus diseases have been reported from the Philippines [47] These are orange leaf, tungro, yellow dwarf, and grassy stunt There is also evidence that several so called physiological diseases known to occur widely in southeast Asia for many years are caused by viruses [47] These include 'mentek' disease in Indonesia, "penyakit merah' in Malaysia, and "suffocating' in Taiwan Little is known about virus diseases in rice in India It now appears that viruses are the cause of some of the major disease problems in south and south east Asia

The virus diseases of rice in southeast Asia have been most extensively studied in the Philippines There tungro appears to be the most damaging of the virus diseases It has also been found in Thailand and Taiwan The symptoms associated with tungro are yellowing of the leaves and stunting of infected plants The varieties Tjeremas, Peta FB 24, and Gam Pai appear to be resistant or tolerant [20] Taichung Native 1 is susceptible The tungro disease is transmitted by a leafhopper Varieties may be screened for resistance by permitting viruliferous leafhoppers to feed on the plants (Fig 5 13) Leafhoppers reared in the glasshouse from eggs are virus free The leafhoppers are permitted to feed on virus infected plants and then placed on the plants to be tested for virus resistance

Rice plants on which the viruliferous leafhoppers have fed are then scored for resistance

Research to identify virus diseases that may be present needs to be intensified in all of the rice growing areas of south and southeast Asia After the virus diseases are identified sources of resistance must be located and genes for resistance incorporated into locally adapted varieties of rice

D STEM ROT Stem rot is caused by the fungus, *Leptosphaeria salvinii* and *Helminthosporium sigmoideum* The disease is widespread throughout southeast Asia Symptoms are the appearance of spots on the leaf sheath at the surface of the water and dark coloured internodes Infected culms become weak and lodge and produce only lightweight heads Infection usually occurs through wounds Information on resistance in India and other countries of south and southeast Asia is inadequate but tolerance is found in BPI-76, Peta, and several ponlai varieties

E BROWN SPOT Brown spot, caused by *Helminthosporium oryzae*, is a common rice disease in many rice growing areas Brown spot produces seedling blight and spotting on the leaves, hulls and kernels Grains on infected plants are light in weight and poor in quality Not much attention has been given to breeding for resistance since brown spot is generally severe only in fields with poor soils and poor cultural management In India the varieties BAM 10, T 141, and CH 13 are reported to be resistant [15] A single dominant gene was reported to control resistance in a study made in India, while polygenic control was reported from the U S A [11]

F OTHER DISEASES Bunt of rice (*Neovossia horrida*), and false smut (*Ustilaginoidea virens*) are two other common, though less important, diseases Information regarding resistance to these diseases are not available Another disease of some importance in a few countries is the narrow brown leaf spot disease (*Cercospora oryzae*) Single or duplicate genes appear to control resistance to this disease Resistance to nematodes also deserves attention

Insect Resistance. Insect pests cause a major loss to the rice crop, and are more serious than diseases in some countries Yet, not much progress has been made in breeding for insect resistance in rice Most studies on breeding for insect resistance have been confined to stem borers although some work has been done on stem maggots (*Chlorops oryzae*) in Japan

A STEM BORERS Stem borer is a common name for several insect species causing similar damage to the rice plant [51] The most important species in India is *Tryporyza incertulas* Two other species of importance in southeast Asia are *Chilo suppressalis* and *Chilotraea polychrysa* Resistance to stem borer appears to be related to the stem thickness and hardness The varieties Ishwarkora and TKM 6 are resistant in India A number of resistant varieties have been identified at the International Rice Research Institute In general, japonica varieties had greater resistance than indica varieties To supplement natural infestations, egg masses of the stem borer may be attached to the rice plant Resistance to stem borer is dominant over susceptibility and is governed by one or more genes [11 57]

B OTHER PESTS Gall fly (*Pachydiplosis oryzae*) and gundhi-bug (*Leptocorisa varicornis*) are other important insect pests of rice that need attention in resistance to breeding

Quality in Rice. Quality in rice, as with other cereals processed for human food, is a combination of many characteristics The grower is concerned with those characteristics that affect the drying of the rice, its market quality, and its germination In rice used for home consumption, plumpness of grain, freedom from diseased kernels, and cooking quality are also important The rice miller is concerned with the milling characteristics of the rice The processor and the consumer are concerned with its cooking and eating qualities All of these quality characteristics of rice are affected by the variety, but they are also affected by soil, climate, disease, and procedures in harvesting, drying, and processing The breeder needs to give consideration to genetic improvement in the grain characters, and to the milling and cooking characteristics of the rice [3,6 23]

A GRAIN CHARACTERS Grain characters important in a rice variety include seed dormancy, awnness, and pubescence of the hull

Varieties differ in their seed dormancy Varieties without seed dormancy tend to germinate immediately after maturity and sprouting in the panicle before harvest may become a problem if there is rain during the harvest period Generally, japonica varieties are nondormant while indica varieties are dormant Therefore, seed dormancy must be checked carefully in selections made from crosses

involving japonica varieties This may be done by a germination test made immediately after harvest Most of the dwarf strains developed at the International Rice Research Institute have seed dormancy Seed dormancy is reported to be a dominant trait conditioned by two or three genes [11] Presence of seed dormancy may become a problem in areas where two crops of rice are grown and it is desired to sow the second crop immediately after the harvest of the first crop In this case seed dormancy may be broken by exposure of the seed to a temperature of about 50 degrees Centigrade for a period of 4 to 5 days depending upon the variety [23] The extent of dormancy may be tested by germinating the rice seed at varying periods starting immediately after harvest

Most indica varieties are awnless, which is favoured for handling during harvesting, threshing, and cleaning, where these operations are done manually as in India and other countries of south and southeast Asia Most tropical varieties, including those from India are pubescent whereas most U S A varieties are glabrous Glabrous or smooth hull is conditioned by a single recessive gene [11] A glabrous or smooth hull is preferred to a pubescent hull when handling rice in threshing, drying, dehulling and processing

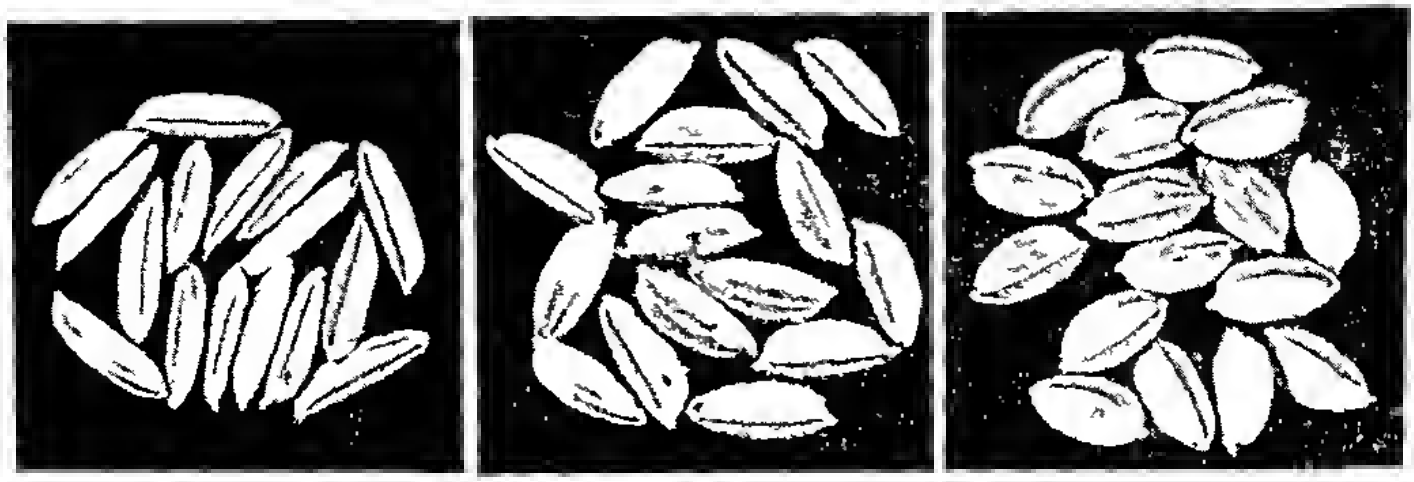
B MILLING CHARACTERISTICS The unhusked rice grain received by the miller is known as *rough rice* or *paddy* The miller converts it to *brown* rice by shelling off the hulls, and to *milled* rice by scouring off the outer bran layers The value of the rough rice depends largely upon its milling quality, which is determined by the percentage of *head* and *total* rice that is obtained from rough rice *Head* rice refers to the whole grains and the large broken pieces (three-quarters size or larger) *Total* rice refers to all the rice recovered after the milling process, both whole and broken kernels Small and medium grain varieties give larger mill yields than long grain varieties *Parboiled* rice is rough rice that has been soaked and steamed or heated in water before milling to facilitate removal of the outer husk or hull Parboiling aids milling by reducing the breakage during milling and the yield of head rice is thereby increased by as much as 10 percent.[16] Also, polishing of parboiled rice does not need to be carried as far and there is less loss of vitamins and other nutrients in the process The average milling outturn of rice is around 65 to 70 percent in improved varieties The percentage of outturn is higher in parboiled rice than in raw rice

Rice grains of different varieties may be classified into (*a*) long, (*b*) medium or (*c*) short, according to length of grain (Fig 7 14), and (*a*) bold, (*b*) medium, or (*c*) slender, according to the ratio of length to width [12] Rice grains of different varieties may also be compared for appearance by noting the presence of "white bellies", translucency, and the breakage at the basal-ventral end of the grain which is referred to as the condition of the "eye" Chalky and mottled grains are undesirable The long grain varieties have a slightly greater husk percentage and also tend to break more easily in milling than medium or short grain varieties Long grain varieties with a uniform translucency in the endosperm and a bright lustre have more "eye appeal" to many, but not all, consumers in certain areas

Plant breeders need to evaluate the milling properties of the varieties and strains of rice they produce In the early stages of testing only a small quantity of seed is available, so quality evaluation procedures must be scaled down to utilize the small quantity of seed which the breeder can spare. An estimate of total milled rice may be obtained by hulling a 10 gram sample of rough rice in a McGill sheller and determining the percentage of hulls removed [2] The brown rice samples obtained are then milled and polished in a test tube miller (Fig 7 15) The milled rice obtained may be examined for grain size, shape, translucency, and chalkiness,[20] and evaluated for cooking characteristics

C COOKING CHARACTERISTICS Cooking characteristics of rice varies with the variety Some varieties remain dry and flaky when cooked, others are sticky or chewy Preference for a particular kind varies in different areas and in different countries The breeder needs to know the preference of the people in his area and the cooking characteristics of the varieties he produces [8 12]

The dry-flaky cooking characteristic of rice is usually found in varieties with a high percentage of amylose, a medium high gelatinization temperature, and maximum viscosity, of the cooked rice paste when cooled to 55 degrees Centigrade The varieties with low amylose and low gelatinization temperatures tend to be sticky and cohesive when cooked, absorb more water and thus have more



7 14A 7 14B 7 14C

Fig 7 14 Grain types in rice A Long grain B Medium grain C Short grain

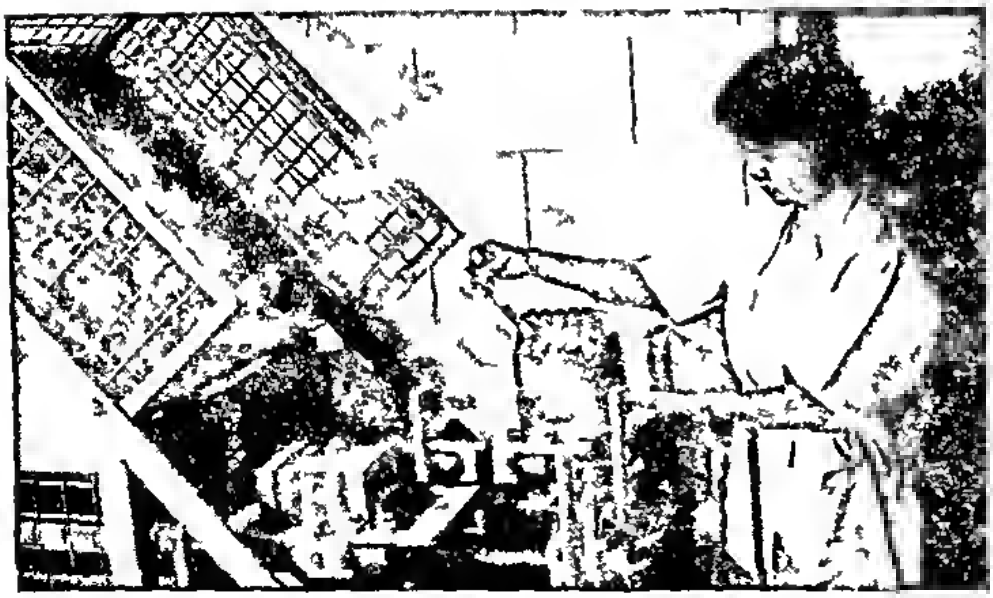


Fig 7 15 Milling experimental rice variety samples in the test tube miller at the International Rice Research Institute

volume after cooking and also cook faster These characteristics are preferred in many areas of tropical Asia In general the long grain indica varieties tend to have higher gelatinization temperatures[17 36] and lower amylose[72] than the medium or short grain indica varieties

Adaptation to Special Conditions and Uses Rice is grown not only on low and high lands in the plains, but it is also grown in high altitudes up to 6 000 feet or more above sea level in saline areas along the sea coast in drought affected areas as a rainfed crop and as deep water rice in submerged areas[16] The varieties normally developed for the plains areas are not adapted to growing in the other areas Different varieties are needed for each of these specific environmental conditions Besides daylength temperature also plays an important role in adaptation of rice varieties to high altitudes Some of the japonica varieties with earliness photoperiod insensitivity and low thermosensitivity are grown at high altitudes Breeding for tolerance to salinity in India has resulted in the development of varieties which can tolerate saline levels of 0 5 to 1 0 percent The floating varieties of deep water rice are of long duration photoperiod sensitive and have rapidly elongating internodes Varieties that

can withstand depths of water from 3 to 5 metres are available

Very fine seed size and scent or aroma add to the quality of rice used for delicacies like polao and pudding Inheritance of scented grains is stated to be controlled by one, two or three complementary genes

Various kinds of special purpose rices are used in India as well as other rice growing countries of southeast Asia The rice flour of certain glutinous types is used for various kinds of pastry products Similarly specific types of rice are used for puffed rice, popped rice soft rice, and chira' Very little attention has been paid to the improvement of these different types of rice since they are of minor importance compared to the major problem of developing high yielding rice varieties for food production

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8

Breeding Maize

Maize is the leading cereal crop in the Americas In the United States it occupies nearly one-fourth of the total crop land and has a value double that of wheat the second most important crop In India, maize occupies fifth place in acreage and fourth place in production among the cereals grown Maize is grown on limited acreages in other countries of south and southeast Asia Maize is a relatively recent introduction to this area of the world, apparently being brought to southeast Asia from America by Portuguese traders about the sixteenth century With the high yield potential of maize, the development of maize hybrids adapted to this area, and education on the utilization of maize as food, the acreage and importance of maize here will no doubt increase in the future

HISTORY AND ORIGIN OF MAIZE

The maize plant is native to the Americas Remains of prehistoric maize dating back to 3,000 to 5,000 B C have been found in caves in Mexico [33] The basic botanical characteristics of the maize plant from these caves indicate it has not changed during this period Only size and productiveness of the plant parts have increased during the domestication of the maize plant This is further evidence of the effective improvement in maize carried out by the Red Indians of America It was their basic food plant when Columbus discovered America and is still the most important cereal food crop in Mexico, Central America, and many countries in South America Maize is one of the oldest of the cultivated crops It is no longer capable of survival in the wild form and can be grown only under cultivation

Maize, *Zea mays*, is the only species in the genus *Zea* Its diploid chromosome number is $2n=20$ It has two close relatives, gamagrass and teosinte Gamagrass (*Tripsacum*) grows wild in the eastern and southeastern sections of the United States and in Central and South America Species of *Tripsacum* with 18 and 36 pairs of chromosomes are known Teosinte (*Euchlaena*) is native to southern Mexico and Guatemala and is generally regarded as the closest relative of maize The annual form of teosinte has 10 pairs of chromosomes, the same number that is found in maize A perennial species of *Euchlaena* with 20 pairs of chromosomes is also known Maize crosses readily with teosinte By the use of special techniques, crosses have also been made between maize and gamagrass [25]

Two locations have been suggested as the possible origin of maize These are (*a*) the highlands of Peru, Equador, and Bolivia, and (*b*) the region of southern Mexico and Central America Many types of maize have been found in both areas which may be grouped into distinct races [5 74] Several theories to account for the origin of maize have been advanced [40 72] One theory suggests that maize developed from a primitive pod corn, that teosinte originated as a hybrid between corn and *Tripsacum*, and that modern races of maize have originated through introgression of teosinte into maize [40] However, with present information neither the place nor the mode of origin of maize can be stated with certainty

POLLINATION IN MAIZE

An understanding of the methods of breeding maize is dependent upon a knowledge of its pollination and the effects of the pollination method upon the genetic composition of the maize plant Maize bears monoecious flowers with staminate flowers produced in the tassel and pistillate flowers on the shoot Pollination is accomplished by the transfer of pollen from the tassel to the silks About 95 percent of the ovules on a shoot are cross-pollinated and about 5 percent are self pollinated Most of the pollen that pollinates an ear of maize

usually comes from stalks in the immediate vicinity, but pollen may be carried by the wind for distances up to one kilometre

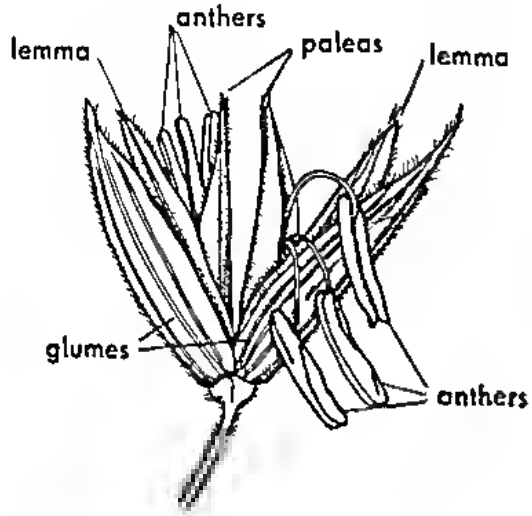


Fig 8 1 Staminate spikelet of maize

The main stem of the maize plant terminates in a tassel bearing two flowered staminate spikelets each flower having three stamens (Fig 8 1) [21] As the tassel flowers open the anthers are pushed out by the elongating filaments (Fig 8 2) and pollen grains are emptied from the extruded anthers It has been estimated that a single tassel from a normal plant may produce as many as 25 000 000 pollen grains or an average of over 25 000 pollen grains for each kernel on an ear with 800 to 1 000 kernels [20] Pollen shedding begins one to three days before the silks have emerged from the husks of the same plant, and usually continues for a period of several days after the silks are ready to be pollinated Hot dry weather tends to hasten the pollen shedding

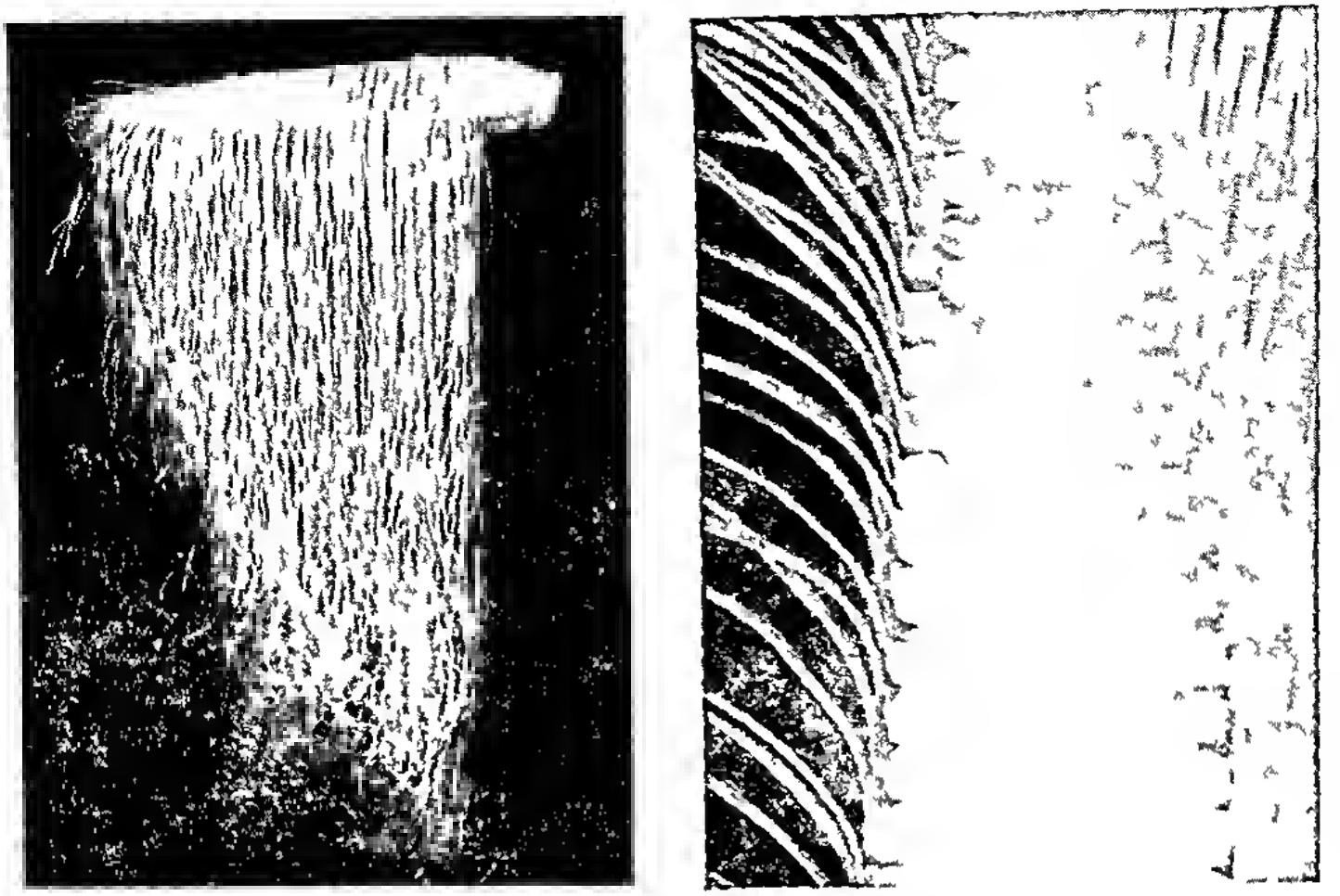
The ear shoots arise as branches from nodes about midway of the stalk Each shoot is composed of a shank from which the husks arise and terminates in the ear on which the pistillate flowers are borne The spikelets are borne in pairs and since each spikelet normally produces one fertile ovule, there is an even number of rows of kernels on the ear A second ovule is present in the spikelet, but does not normally develop Fertilization of the second ovules produces crowded and irregular kernels on the ear Fresh silks function both as the stigma and

Fig 8 2 Tassel branch of maize showing anthers exserted from a staminate flower

the style (Fig 2 10) and are receptive to fresh pollen throughout their entire length (Fig 8 3) Severe drought may delay the emergence of the shoots Fertilization of the ovule usually occurs within 12 to 28 hours after the silks have been pollinated [43]

Under favourable conditions pollen may retain its viability for 18 to 24 hours, but it may be killed in a few hours by heat or desiccation A hot dry wind may injure the tassel so that it does not shed pollen, or it may reduce the silk moisture so that pollen grains will not germinate

Maize propagated from seed that has been produced by uncontrolled pollination is commonly referred to as *open pollinated maize*



8 3A 8 3B

Fig 8 3 Ear shoot of maize A With husks removed A silk is attached to the tip of each ovary A fresh silk is receptive to pollen throughout its entire length B Cross section of ear shoot showing ovaries with silks attached

GENETIC AND CYTOGENETIC STUDIES OF MAIZE

No other crop has been subjected to such intensive genetic and cytogenetic studies as maize [51] Nearly 500 different genes have been identified [73] and linkage maps have been constructed to show the relative position of numerous genes on each of the 10 chromosomes (Fig 3 4) A more or less uniform system of genetic nomenclature has been used throughout these studies As nearly as possible, characters have been given a name which suggests one of its features The gene symbol consists of the initial letter of the name, or the initial letter and some other appropriate letter in the name Genes in an allelic series are differentiated by superscript letters Genes with phenotypically similar characters are given the name and differentiated by subscript numbers Examples are as follows

Character	Gene symbol	Chromosome on which gene is located
Pericarp and cob colour	P	1
Sugary endosperm	su	4
Red pericarp and red cob colour	P^{rr}	1
White pericarp and red cob colour	P^{wr} (allelic to P^{rr})	1
Yellow endosperm, 1	Y_1	6
Yellow endosperm 2	Y_2	5

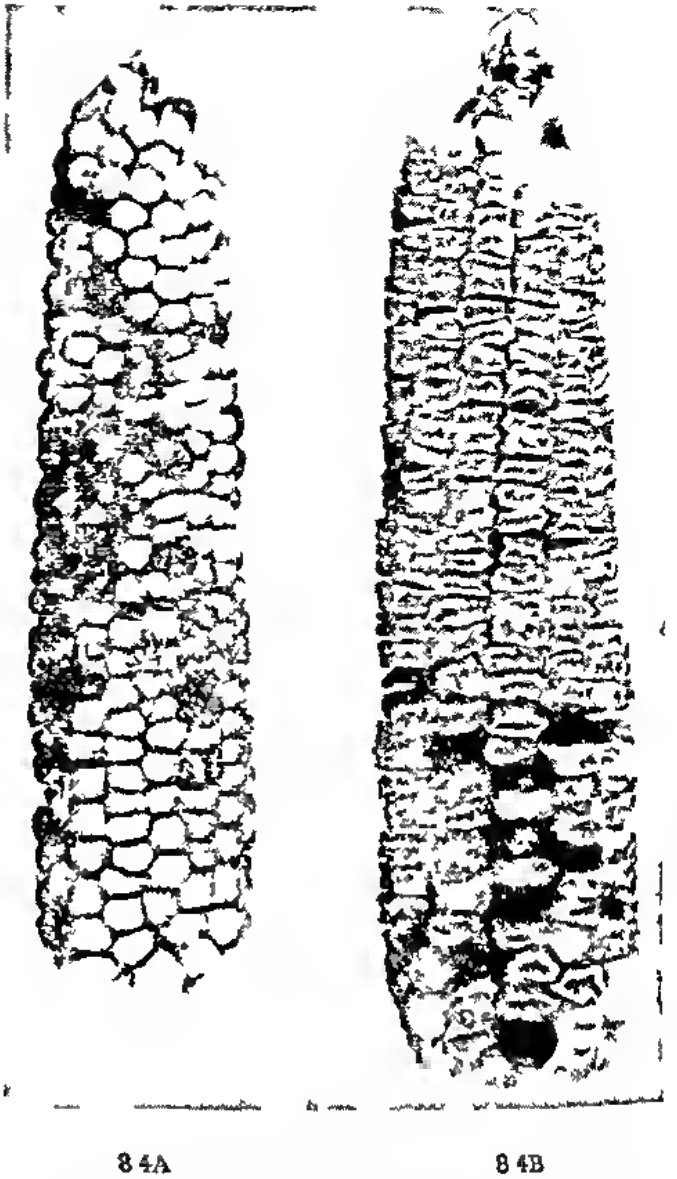
Many genetic studies have been made with maize because (*a*) it is a widely grown crop, (*b*) either cross- or self pollinations are made easily, (*c*) large numbers of seed are obtained from one ear, (*d*) many easily observed hereditary characteristics are available to study, and (*e*) maize contains many recessive characters which are exposed through inbreeding as a result of its being normally a cross-pollinated crop The fact that the system of breeding hybrid maize developed from inheritance studies has also stimulated further genetic investigation with this crop

Xenia Xenia is the immediate effect of pollen on the developing kernel When yellow maize pollen fertilizes an ovule of white maize, a light yellow kernel develops When white maize pollen fertilizes an ovule of yellow maize, a medium yellow kernel develops This phenomenon results because the yellow colour is found only in the horny starch of the endosperm as may be observed by cutting a kernel of maize lengthwise The endosperm develops after the fusion of the second sperm with the diploid polar nuclei and has a triploid chromosome number The yellow endosperm colour is conditioned by a dominant gene (*Y*) The recessive alleles (*yy*) produce a white endosperm Since the endosperm receives two sets of chromosomes from the polar nuclei, it will receive two genes for *Y*, or *y*, dependent upon the character of the mother plant, to one gene for *Y*, or *y*, from the pollen The effects that pollinations of the polar nuclei with different kinds of pollen have on the developing kernel may be outlined as follows

Colour genes in polar nuclei		Colour genes in sperm		Colour genes in endosperm
YY	+	*Y*	=	*YYY* (deep yellow)
YY	+	*y*	=	*YYy* (medium yellow)
yy	+	*Y*	=	*Yyy* (light yellow)
yy	+	*y*	=	*yyy* (white)

Y, yellow gene, *y*, white gene

Other characters which exhibit xenia effects include purple vs white colour in the aleurone (outer endosperm layer) and starchy vs sugary kernel type (Fig 8 4)



8 4A 8 4B

Fig 8 4 Xenia in maize A White maize partly pollinated from plant with purple seed B White sugar maize partly pollinated with white and purple field maize

HETEROZYGOUS NATURE OF OPEN-POLLINATED MAIZE

The heterozygosity of cross pollinated crops was discussed in Chapter 4 Maize is a typical cross pollinated crop Conceivably, every seed on an ear of open pollinated maize may have a different pollen parent It is doubtful that any two seeds on the same ear have exactly the same genotype Therefore, each plant is a separate hybrid with different individual characters, and a field of open-pollinated maize is a mixture of many complex hybrids (Fig 8 5) [57] This results in much variation within a single open pollinated variety For this

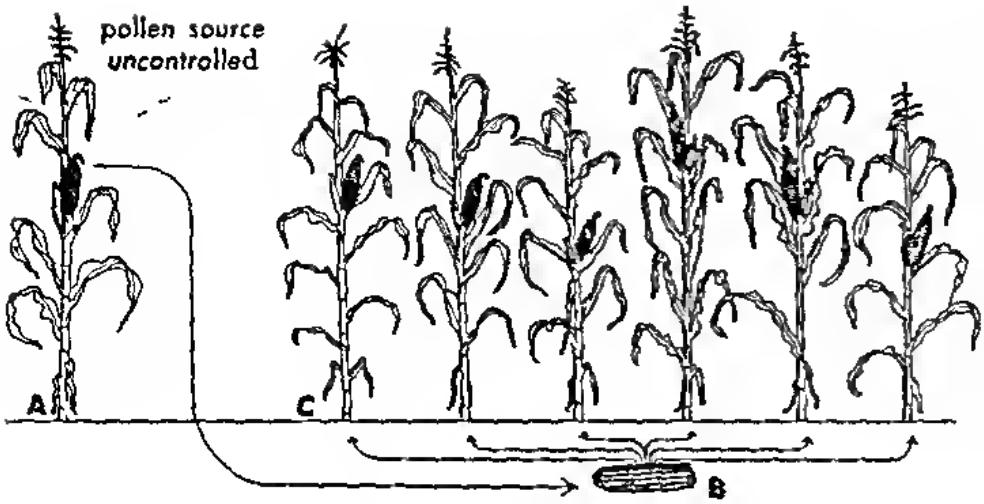


Fig 8 5 Open pollinated plant of maize and its progeny A Plant from an open pollinated variety B Ear from open pollinated plant Each kernel came from a separate fertilization The kernels are related from the female side but may be quite unrelated on the male side, the pollen having come from many plants within the field C Plants grown from seed of an open pollinated variety of maize The plants vary in height, size of ear etc , but on the average retain the general type of the parent variety

reason a variety in open pollinated maize has a far greater range in genetic variability than a variety in a self pollinated crop such as wheat or rice

METHODS USED IN BREEDING MAIZE

Varieties in open pollinated maize have been developed largely by *mass selection* In the U S A., two other methods of breeding open pollinated maize, *ear to row selection* and *variety hybridization* were tried but were never widely used Since the development of *hybrid maize* most of the efforts have been directed toward this method of breeding In India and some other areas *synthetic varieties* and *germ plasm complexes* are being developed either for use as varieties or as sources of germ plasm for further breeding

Introduction and Germ Plasm Collections. Maize was introduced into India and other countries of south and southeast Asia more than 200 years ago Present evidence indicates that the range of genetic material introduced into this area was relatively narrow Currently, germ plasms are being introduced into the coordinated maize breeding programmes of India and southeast Asia from Mexico, Central America, and southern Corn Belt of the U S A , Kenya, and other countries These are being used in the development of germ plasm complexes, synthetics, and hybrids adapted to the different production areas of south and southeast Asia

Since maize is indigenous to the new world, introduction has not been an important factor in the development of varieties and hybrids in that area Large collections of maize germ plasm have been made throughout Mexico and Central and South America in order that representative types of the original races of maize[5 74] in those areas will not be lost as native maize is replaced in cultivation by improved varieties and hybrids Also, representative collections of the open pollinated varieties of the U S A are being maintained Cooperating in this programme are the National Academy of Sciences, U S A , the U S Department of Agriculture, maize breeders in Mexico and various countries of Central and South America, and the Rockefeller Foundation (Fig 8 6) [9] Maize germ plasm collected in this programme is contributing to the rapid development of the maize breeding programmes in India and southeast Asia

BREEDING OPEN POLLINATED MAIZE

Mass selection is the principal method of breeding open pollinated maize Most of the important varieties of open pollinated maize in the Americas originated by this method of breeding, either through natural selection, or by objective selection by man Many were developed by farmer breeders who followed the practice of mass selection in the process of maintaining their seed stocks

Mass Selection In the mass selection of breeding maize, ears are chosen on the basis of plant and ear characteristics [25 29 53 55 84] Seed shelled from these ears are mixed and planted *en masse* The ear is the unit of selection because of the necessity and convenience in handling it. Mass selection is used both as a method for maintaining existing varieties of open pollinated maize and for developing new varieties Each cultivator who selects ears of maize

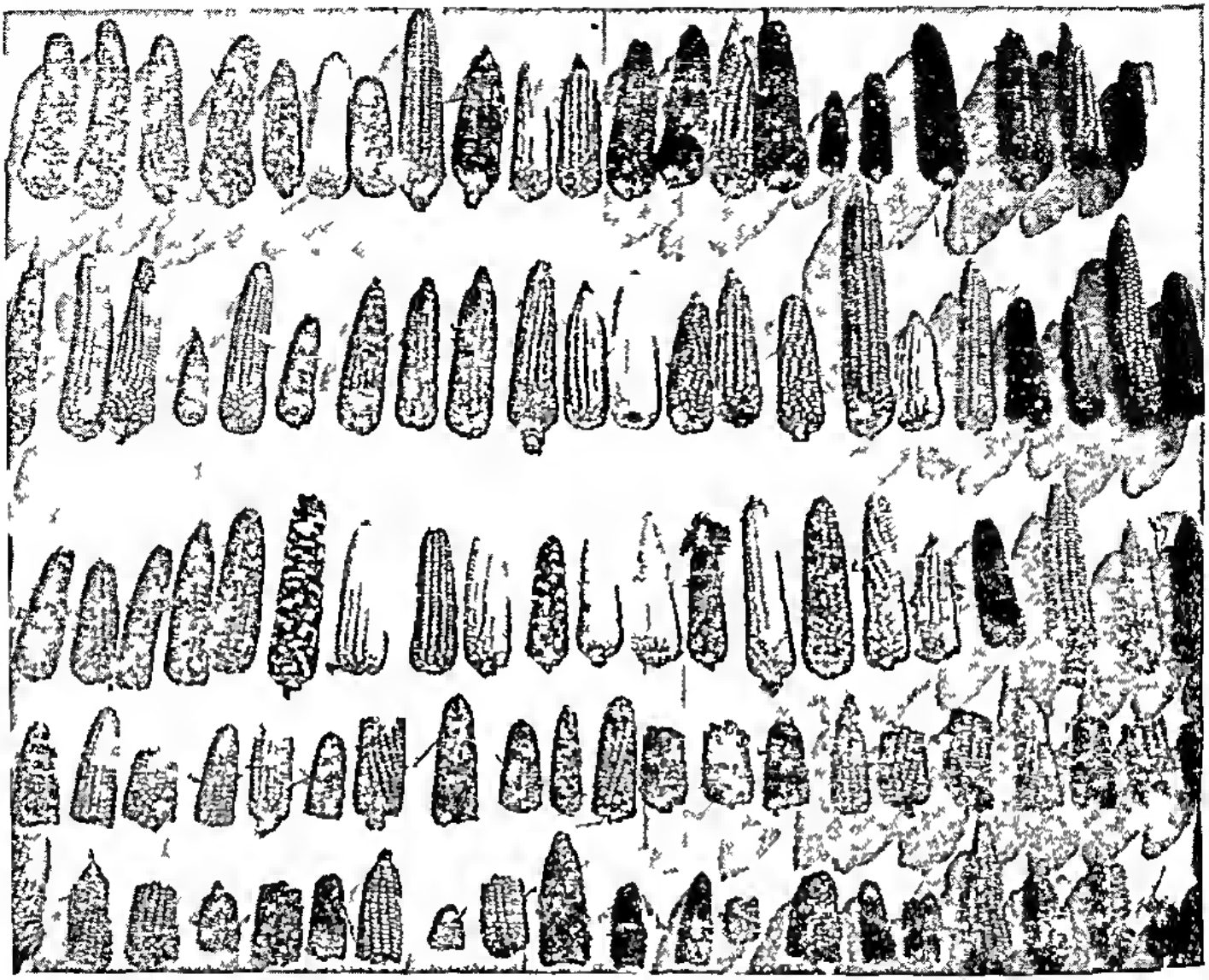


Fig 8 6 Part of the collection of various kinds of maize from Guatemala The United States Department of Agriculture in cooperation with the Rockefeller Institute and other organizations is collecting native strains of maize from Mexico Central America and South America These collections will be maintained in a viable condition as germ plasm reserves for possible use by maize breeders in the future

to plant his next year's crop becomes a breeder, and he can change the character of the maize he grows by selecting for a specific type or characteristic

In the United States, many productive and adapted varieties of maize were developed by mass selection [25 53 64] By mass selection it was possible to modify plant type maturity, kernel characteristics, and chemical composition Selection could be made for long or short ears, rough or smooth indentation of kernels, or other easily recognizable characteristics By rigorous selection the appearance of the maize plant and ear could be changed within the limits of the genetic variability of the variety, which in most varieties appeared to be quite wide Selection was useful in adapting varieties to new production areas or in developing varieties for special purposes In Mexico and in Central America selection over the centuries that maize was being domesticated was effective in the formation of distinct races of maize, with specific characteristics and adaptation to special conditions and climatic areas [5 74] In southeast Asia, mass selection has been practiced to maintain open pollinated types and, consciously or by chance, different varietal types

have emerged in different production areas While the yield potential of most types have been quite low this may have been the result of the limited germ plasm resources originally introduced into Asia and the fact that selection was usually practiced under conditions of poor culture and low soil fertility

Mass selection was not generally considered effective in earlier years for increasing the yield of an adapted variety The ineffectiveness of mass selection for increasing yield resulted from (*a*) the breeder s inability due in part to poor experimental techniques to recognize whether a particular plant was superior due to its genotype or to the specific environment in which it was growing (*b*) superior plants being pollinated from both superior and inferior plants so that the high yield potential of a plant was not reproduced in all of its offspring and (*c*) the fact that rigorous selection for specific plant characteristics often led to inbreeding and thus actually decreased yields The results of many experiments[28 52] demonstrated rather conclusively that seed selection based on minor visible characters was of no value for determining the productiveness of seed ears There was an indication that in open pollinated maize most progress may be made by selecting for (*a*) vigorous strong plants (*b*) large, sound well developed ears (*c*) ears from disease free plants and (*d*) proper maturity

Ear-to-Row Breeding In an effort to improve the efficiency of selection an ear to row method of breeding maize was started at the Illinois Agricultural Experiment Station about 1896[25 29 53 61 64] The essential features of the ear to row system of breeding as it was later developed are as follows

1 Fifty to one hundred ears are shelled separately Part of the seed from each ear is planted an ear to a row The remainder of the seed is labelled and kept

2 Each row is scored for desirable characters and for yield and the best rows are selected

3 Remnant seed from ears producing the ten to twenty best rows is used to plant a plot the second year Ears are selected from this plot and the process is repeated

After several years of extensive testing it became apparent that plant or seed characteristics with high heritability and those that could be evaluated accurately by visual observation could be altered rapidly with the ear to-row method of breeding just as with mass selection This was illustrated by changes in a Burr White variety after ten years of selection in Illinois for high and low oil content and for high and low protein content (Table 8 1)[29 61] For characteristics with low heritability and those that could not be evaluated accurately by visual observation the method has proved ineffective Yield was not improved apparently by the ear to row method of breeding The conclusions drawn were that the ear to row method as well as mass selection was ineffective in increasing yield because the high yielding ears were superior chance hybrids which did not breed true[55] and that poor field plot techniques made it impossible to identify with accuracy the high yielding rows[36]

Table 8 1 Average Oil and Protein Content of Burr White Maize and Four Strains Selected from Burr White by the Ear to Row Method[a]

Variety and strains	*Oil content* (%)	*Protein content* (%)
original Burr White parent variety	4 70	10 92
high oil strain after 10 years ear to row selection	7 37	—
low oil strain after 10 years ear-to row selection	2 66	—
high protein strain after 10 years ear to row selection	—	14 26
low protein strain after 10 years ear to-row selection	—	8 64

[a] *Illinois Agricultural Experiment Station Bulletin* 128[61]

A New Look At Some Old Methods Although the opinion was prevalent in earlier years that no progress was being made in improving yield either by mass selection or ear to row breeding there was no critical experimentation by which the procedures could be carefully evaluated Furthermore interest in the potential of hybrid maize at that time caused most maize breeders in the U S A to lose interest in the mass selection and ear to row breeding procedures

Some recent research, however, has thrown new light on the effectiveness of mass selection for improvement of varieties of open pollinated maize [35] An average gain of 3 9 percent per year over the original open-pollinated variety, Hays Golden, was obtained over a four year period[15] in a mass selection experiment These and other recent data indicate that progress may still be made in obtaining higher yield by mass selection within many of the older open-pollinated varieties This is of importance for maize breeders in areas of the world where hybrids have not yet been established The new look at mass selection is possible because plant breeders today have improved experimental techniques for growing maize and more refined statistical procedures for measuring improvement Knowledge of quantitative inheritance, also, provides a better understanding and interpretation of the genetic factors contributing to yield By the use of this knowledge it has also been possible to develop more accurate techniques for handling ear-to row selection in open pollinated maize which should provide for intensification of favourable genes for yield or other characters without undue inbreeding [36] Utilization of these new techniques in mass selection and ear-to row breeding may lead, not only to new varieties of open pollinated maize, but also to the development of germ plasm pools which may be useful in breeding improved maize hybrids

Variety Hybridization. Hybridization between varieties, either intentional or accidental, was responsible for the origin of many commercial varieties of open pollinated maize [53] Such hybridization added to genetic variability and often new varietal types could be evolved

In 1880, Dr Beal, at the Michigan Agricultural Experiment Station in the U S A, described an experiment in variety hybridization[3] in which one variety was detasseled and pollinated by a second variety grown in an adjacent row An increase in yield was obtained in the hybrid progeny A plan by which farmers could produce their own crossed seed was later outlined However, variety hybridization never became popular with farmers in the U S A, probably because it was too advanced for farmers of that period

HYBRID MAIZE

Early attempts to improve the yield of open-pollinated maize in the U S A were mostly disappointing, although varieties adapted to various production areas had been developed While it was possible to develop many different varieties or to change the characteristic appearance of a variety by continued selection, little progress was made in raising the inherent yielding ability of a well established variety This failure to improve the yield stemmed from the heterogeneous nature of open pollinated maize and the poor plot techniques used at that time A field of open pollinated maize is composed of both inherently high- and inherently low-yielding plants The inherently high yielding plants are the result of favourable gene combinations But the favourable gene combinations are not always reproduced in the progenies of the high yielding plants since the plants are fertilized by pollen produced on both good and poor plants all of which are highly heterozygous Until the development of the concept of hybrid maize, there was no available method by which the genotype could be sufficiently controlled so that only inherently high-yielding plants would be grown within a single field of maize

History of Hybrid Maize. A new era in maize breeding began in 1909 when Dr G H Shull suggested a method for producing hybrid maize seed [69] The previous year Dr Shull had reported[51] that an ordinary field of maize is composed of many complex hybrids which decline in vigour with inbreeding, and that the breeder should strive to maintain the best hybrid combinations As a result of inbreeding and crossing studies, Dr Shull outlined a plan in 1909 for (*a*) inbreeding to establish pure lines and (*b*) crossing the pure (inbred) lines to produce uniformly productive hybrid lines [53]

Dr Edward East, who had worked at Illinois and the Connecticut Agricultural Experiment Station in the U S A, also reported on the inbreeding of maize in 1909 [31] His results were similar to those of Dr Shull At first it appeared that the method of breeding hybrid maize would not be practical because the cost of producing the hybrid seed was so high The problem was solved when Dr D F Jones in 1918 suggested crossing two vigorous single cross strains and producing "double cross" seed [28] This step made production of hybrid maize seed economically feasible The first commercially grown double cross maize was a Burr-Learning hybrid produced at the Connecticut

Agricultural Experimental Station and grown in Connecticut in 1921 (Fig 1 5) In 1924 a single cross developed by H A Wallace was sold in Iowa under the name Copper Cross

It was not until the late 1930's, nearly thirty years after Dr Shull's original suggestion for producing hybrid maize seed, that maize hybrids became extensively used in the U S Corn Belt There were several reasons for this delay In the beginning many breeders were slow to grasp the potential possibilities that the method of breeding offered This can be easily understood if we remember that genetics was at that time a new science It was necessary first to develop the genetic background to explain the theory behind the new breeding procedures Starting about 1920, maize breeders in the U S A abandoned most efforts to improve open pollinated maize and began in earnest to inbreed maize and to fit the inbreds into satisfactory hybrid combinations [16] Years of work were required before high-yielding hybrids adapted to the different production areas in the U S A could be put into production Once adapted hybrids were available, the response of the American farmer to hybrid maize was phenomenal Within the ten year period from 1936 to 1945, the use of hybrid maize in the U S Corn Belt increased from less than 5 percent to over 90 percent of the total acreage planted Now 100 percent is planted to hybrids

One of the most significant facts about hybrid maize is that it developed as a result of research in a basic science, *genetics* Dr Shull, working in a private research institute, the Carnegie Institution of Washington, Cold Spring Harbor, New York, was not a maize breeder He was interested in learning facts about inheritance in plants He chose the maize plant for study As a result of his studies and the method of breeding that he envisioned, millions of quintals are now being added to the world's total production of maize each year This is an outstanding example of the practical use that may some day result from theoretical studies in a basic science

What is Hybrid Maize? Hybrid maize is the first generation progeny from a cross involving inbred lines [18,25,29 53 55 63,64] The breeding of hybrid maize involves (*a*) development of inbred lines by controlled self pollination, (*b*) determination of which inbred lines may be combined into productive crosses, and (*c*) commercial utilization of the crosses for seed production An explanation of the principles and procedures employed in the development of maize hybrids and in the commercial production of hybrid seed will be presented first This will be followed by a discussion of the methods for breeding new improved hybrids and the objectives important in their breeding

A INBRED LINES An inbred line is a "pure line" developed by self pollination and selection until apparently homozygous plants are obtained This usually requires five to seven generations of inbreeding Since maize is normally cross pollinated, pollination must be controlled in each generation, and the silks must be pollinated by hand with pollen collected from the tassel After an inbred line is developed, it may be maintained by self-pollination Sib-pollination (mating of plants within the same inbred line) may be used for a limited number of generations to increase an inbred line

Inbred lines were developed originally from open-pollinated varieties If a maize plant from an open-pollinated variety is selfed, the progeny will be reduced in vigour as compared with the parent plant Additional reduction in vigour may be noted with each selfed generation until a homozygous or true-breeding line is developed About one-half of the total reduction in vigour comes in the first generation of selfing, the remaining loss being halved with each successive generation so that losses are small after three to five generations (Fig 3 8) In addition to loss of vigour, individual plants in the early selfed progenies exhibit many faults such as reduction in plant height, tendency to suckering, lodging, disease susceptibility, and a wide assortment of other undesirable characteristics (Fig 8 7) The most desirable plants are selected for selfing again in each generation, and the weak, abnormal plants are discarded Striking differences between lines are observed with each successive generation of inbreeding, and the weaker lines are discarded Within lines, plants become more alike After five to seven generations of inbreeding and rigorous selection, vigorous inbred lines, uniform in appearance, are developed Each inbred will have a different combination of genes An inbred is a pure line and is descended by self-pollination from an apparently true breeding plant. Hence, each plant will look exactly like every other plant within the same inbred line.

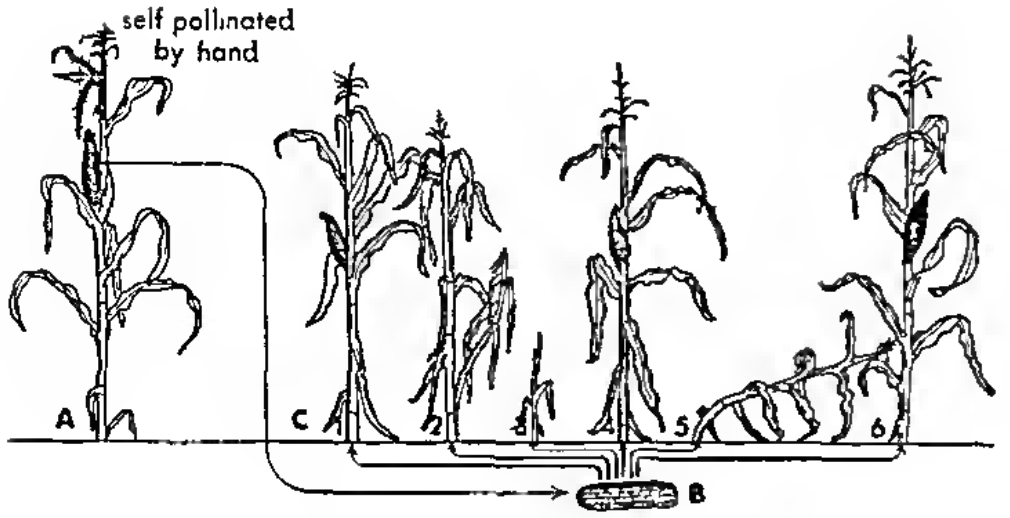


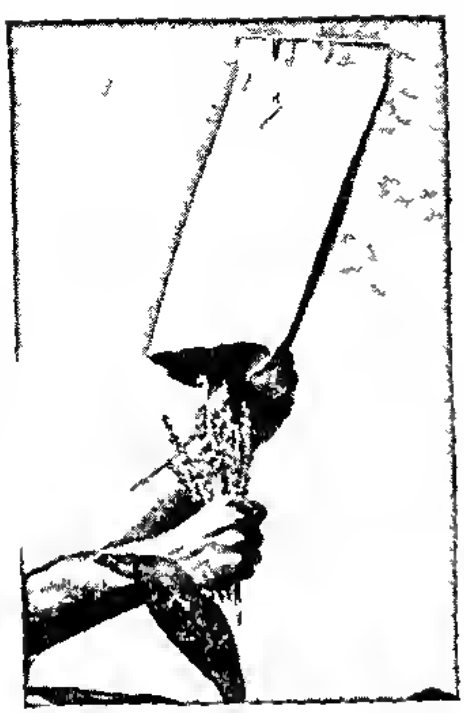
Fig 8 7 Self pollinated plant o maize and its progeny A S plant from open pollinated vane ty B Ear from S_0 plant Th kernels on this ear are relate on both the male and femal sides C S_1 (first generatio selfed) plants Segregation fo plant and ear characters occur in the progeny of the selfe plant Undesirable plants (2 3 5) are discarded Plants possessing desirable characters (1 4 6) are used for further self pollinations Self pollination and selection continue until the line becomes fixed or true breeding This requires five to seven generations

The purpose of inbreeding is to fix desirable characters in a homozygous condition in order that the line may be maintained without genetic change Vigour exceeding that lost during the period of inbreeding is regained in the F_1 progeny when the inbred is crossed with an unrelated inbred During the inbreeding process many undesirable recessive genes that reduce yield, which are masked by their dominant allele in an open pollinated variety, are eliminated as the weak and undesirable plants are discarded The desirable characteristics of the inbreds, such as strong stalks and disease resistance, are transmitted to the hybrid progenies when the inbreds are crossed The most productive hybrids will generally come from crosses of the strongest and most vigorous inbred lines

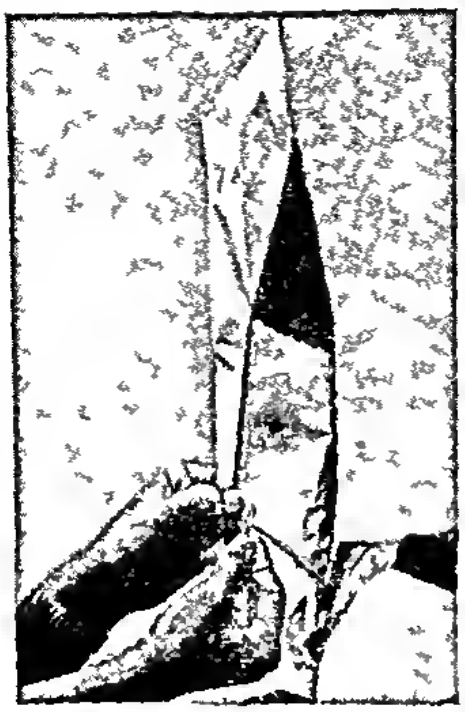
The original selfed or inbred plant is generally referred to as the S_0 (or I_0) plant, and the first generation selfed or inbred progeny from this plant as the S_1 (or I_1) progeny The second generation selfed or inbred progeny is called the S_2 (or I_2), and so on

The technique of inbreeding requires careful attention to prevent natural crossing Details of the procedures may differ with different workers,[25 29] but the essential practices remain the same (Fig 8 8) Ear shoots on the plants to be inbred are covered with a glassine or butter paper bag, about $2\frac{1}{2} \times 6$ inches in size, one to two days before the silks emerge When the silks have emerged and the tassel is shedding pollen the bag is lifted slightly, the ear shoot is cut back with a sharp knife about 1 inch below the tip of the husk and the ear shoot bag is replaced By the following day the silks will grow out to form an even brush about 1 to $1\frac{1}{2}$ inches long for pollination At the same time that the silks are cut back the tassel is covered with a paper bag The following day the pollen is collected in the tassel bag and transferred to the silks This is accomplished by tearing off the tip of the ear shoot bag and quickly pouring the pollen over the fresh silks Care must be taken to avoid contamination with foreign pollen The ear shoot bag is crumpled down and the tassel bag is then placed over the ear shoot and fastened securely Information regarding the cross is marked on the bag Supplies needed for maize pollination are usually carried in an apron for convenience These include a supply of tassel and ear shoot bags, paper clips, a paring knife to cut back the end of the ear shoot, a wax pencil to mark bags, and the field record notebook

A particular inbred line is generally identified by numbers, letters, or a combination of both In India, inbreds developed and released through the Coordinated Maize Improvement Scheme are given the letters CM (indicating Coordinated Maize) and an identifying number Examples are CM 109 and CM 202 Thousands of inbred lines have been developed in various public and private maize breeding programmes since the inception of the idea of hybrid maize Very few of the inbreds developed are good enough to enter into the production of a commercial hybrid Most are discarded somewhere in the testing programme



8 8A



8 8B

8 8C

8 8D

8 8E

8 8F

Fig 8 8 Steps in selfing and crossing maize A Covering the tassel with numbered paper bag Pollen will be collected in the paper bag B The paper bag is fastened securely with a paper clip C Cutting back the ear shoot before the silks emerge to obtain a full brush of silks D After the ear shoot is cut back it is covered with a glass ne or butter paper bag E The following morning pollen collected in the tassel bag is dusted over the silks which have grown out into a brush 1 to 2 inches in length F The ear shoot bag and the numbered tassel bag are now placed over the pollinated ear shoot to protect and identify the developing ear

because they do not "nick" with the inbreds with which they are crossed and fail to produce a satisfactory single cross, or because they have other weaknesses Only a few inbreds are used extensively in commercial hybrid maize seed production

B SINGLE CROSSES A single cross is the hybrid progeny from a cross between two inbreds Since the inbreds used in a single cross are presumably homozygous, the single cross plants are heterozygous for all the gene pairs by which the two inbreds differ A superior single cross regains the vigour and productiveness that was lost during inbreeding and will be more vigorous and productive than the original open pollinated parent from which the inbred lines were derived Not all combinations of inbreds will produce superior single crosses In fact, *the combinations of inbreds that produce superior yielding single crosses are rather rare* The inbred combinations must first be tested, as will be described later under the heading Combining Inbreds into Single and Double Crosses ' to find which may be useful for the production of hybrid seed The increase in vigour and productiveness of a single cross over the parent inbred lines is a phenomenon which is known as *hybrid vigour*, or *heterosis*, and will be discussed later It was for the purpose of utilizing the increased vigour obtained by crossing inbred lines that prompted Dr Shull to suggest his original plan for producing hybrid maize Since all plants within a single cross will have a similar genotype, they will be more uniform in maturity and appearance than open pollinated maize

The technique of crossing to produce single cross seed is not unlike that used in development of inbred lines (Fig 8 8) The shoots and tassels are bagged in the same manner as was described for inbreeding However, the pollen collected from one inbred is used to pollinate the second inbred in the production of a single cross Choice of inbred to be used as the pollen parent and of the one to be used as the seed parent will depend upon which inbred produces the most plentiful supply of pollen and which inbred possesses the best ear and seed characteristics In the commercial production of single cross seed the two inbreds to be crossed are planted in separate rows in an isolated field The female (seed producing) parent line is detasseled, or pollen production of the female line may be prevented by the utilization of cytoplasmic male sterility The female line is then open pollinated from the male (pollen producing) parent line. One row of the male parent is planted to each two or three rows of the female parent

Single cross maize seed is produced on an inbred plant which has been pollinated by a second inbred The single cross seed is usually small in size and irregular in shape Seed yields are low as the inbred plants on which the seed is produced are relatively unproductive For this reason single cross seed is expensive to produce A single cross is identified by the inbreds that go into it An example is ' CM 109 × CM 111"

C DOUBLE CROSSES The double cross is the hybrid progeny from a cross between two single crosses (Figs 4 7, 8 9) Double cross seed is produced on a single cross plant that has been pollinated by a second single cross This is the hybrid seed that is usually sold to the cultivator so that the cultivator grows double cross plants The double cross is a hybrid between two heterozygous single cross parent lines and is not as uniform as the single cross Since the double cross seed is harvested from a productive single cross plant, it is more uniform in size and appearance and is produced in greater abundance and more cheaply than single cross seed, which is harvested from an inbred plant This is the reason for making the double cross

Double crosses may be made by hand pollination in the same way that single crosses are made, or they may be produced by planting the two parental single crosses in an isolated field The female single cross is detasseled before pollen is shed, or pollen production is prevented by the utilization of cytoplasmic male sterility, and then it is pollinated by the second single cross One male (pollen producing) row is planted for each three or four female (seed producing) rows Fewer pollen rows are needed, in proportion to the number of female rows, than when making the single cross because the single cross plants are more vigorous and shed more pollen than inbred plants

Double crosses are usually identified by a name or a combination of a name and numbers The pedigree of a double cross hybrid shows the four inbreds going into the double cross For example, the pedigree of the Indian double cross hybrid, Ganga Hybrid Makka 3, is (CM 109 × CM 110) × (CM 202 × CM 111)

D OTHER CROSSES Inbreds may be combined in ways other than single and double crosses The

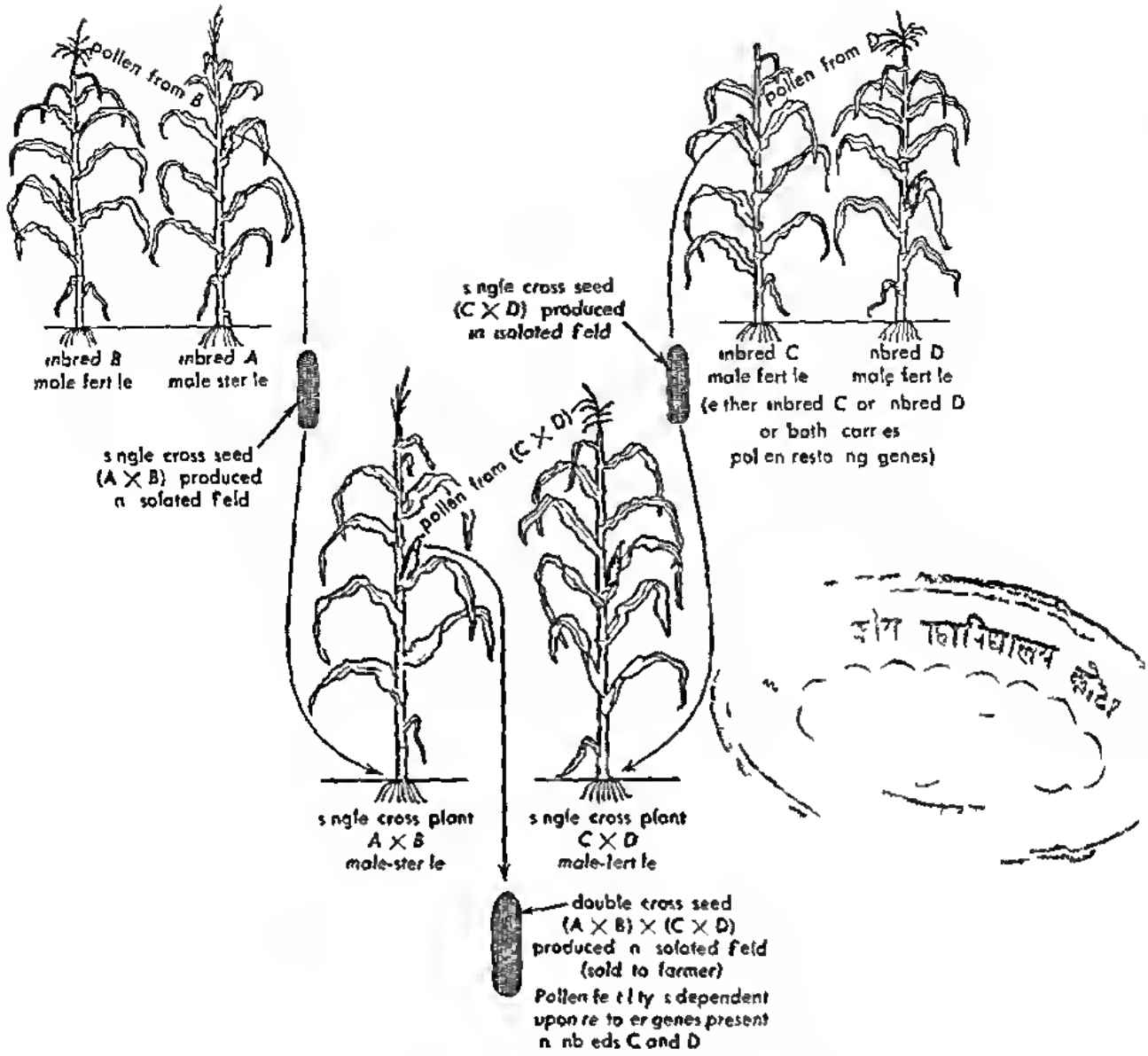


Fig 89 Method utilizing cytoplasmic male sterility in production of single cross and double cross hybrid maize seed In this example only one inbred *A* is male sterile The cytoplasmic male sterility is transmitted to the single cross *A* × *B* and unless pollen restoring genes are carried by the inbreds *C* or *D* to the double cross (*A* × *B*) × (*C* × *D*) also

three way cross is the hybrid progeny between a single cross and an inbred Such a cross may be used when only three good inbred lines are available In India two three way cross hybrids Ganga Safed Hybrid Makka 2 and Hi Starch Hybrid Makka have been released for cultivation Both hybrids involve a single cross which is pollinated by an open pollinated variety

An *inbred variety cross* is a cross between an inbred and an open pollinated variety It is frequently referred to as a *top cross* The inbred variety cross is often used in progeny tests

A *multiple cross* is a combination of more than four inbred lines Multiple crosses are generally less productive than the best double cross combinations that could be put together from the same inbred lines but may have wider adaptation

Heterosis or Hybrid Vigour. Why is hybrid maize more productive than open pollinated maize?[16 51] It has been pointed out that a field of open pollinated maize is a mixture of complex hybrids which vary in their inherent yielding ability The best open pollinated plants are perhaps as good or even better hybrid

binations which maize breeders have put together But it is impossible to reproduce in the progeny of a superior open pollinated plant the exact genotype responsible for its high yield The genotypes of inbreds used in hybrid maize are 'fixed since the inbreds are relatively homozygous and re produce by controlled self pollination or by sib pollination High yielding combinations of single and double crosses can be obtained when inbred lines carefully chosen for their combining ability are mated The desirable combinations may be reproduced because the genotypes of the inbreds remain unchanged and the inbreds can be mated again and again to produce the same hybrid combinations

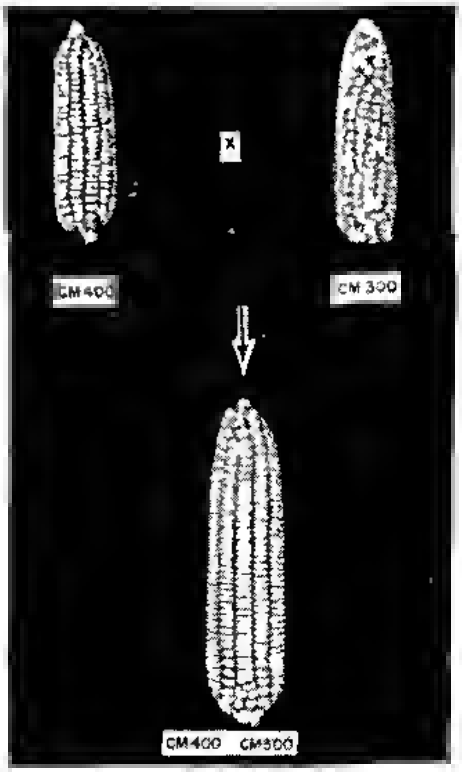
The yields of single crosses from carefully mated inbred lines exceed not only the average yields of the inbreds but also the yield of the open pollinated parent varieties from which the inbreds were derived Such crosses are said to exhibit *hybrid vigour* or *heterosis* (Heterosis is another name for the phenomenon of hybrid vigour) Heterosis may be defined as the excess vigour of the hybrid over its parents [54 59] Heterosis may be exhibited in many ways For example, hybrid maize may have longer ears, more rows of grain per ear, more nodes per plant, more total weight per plant, or greater yield of grain than the component inbred lines (Fig 8 10)

Several theories have been advanced to explain heterosis One theory explains heterosis as the stimulating effect that heterozygous alleles have upon the hybrid plant The theory most generally accepted explains heterosis as the interaction of favourable dominant genes [27] The latter is based on the assumption that heterosis results from the action of dominant genes each of which contributes a small increment to the final yield Each inbred line of maize contains specific dominant genes affecting yield Heterosis is expressed in the hybrid if two favourable sets of dominant genes, which complement each other, are brought together [27] Also, during inbreeding many recessive genes deleterious to the yield of the plant are eliminated

Practices in Hybrid Maize Seed Production. Hybrid maize seed must be purchased by the cultivator for each crop he grows If he should replant the maize he grows, the crop produced from this seed will be reduced in yield and lacking in uniformity This deterioration is a result of inbreeding If extensive acreage of hybrid maize are

8 10A

Fig 8 10 Hybrid vigour in maize A An F_1 hybrid plant and plants of its two inbred parents B An F_1 hybrid ear and ears from its two inbred parents



8 10B

to be grown in any country it is essential then that a source of seed of adapted hybrids be available to the cultivator In the U S A over 8 000 000 bushels (over 2 000 000 quintals) of hybrid seed are planted annually There the commercial demand for so large a quantity of hybrid seed has resulted in the development of numerous specialized private hybrid seed production companies Some are national in scope and have developed their own breeding departments where they develop and test new inbreds and cross combinations and employ many skilled and technical personnel Others are smaller in size and supply only regional or local areas The widescale production of hybrid maize would never have been possible without the effi cient seed production practices that these companies have developed and provided [1] In India hybrid seed is produced by private growers cooperatives and seed companies and also by government farms Foundation seed is supplied by the National Seeds Corporation who also inspects seed production fields and provides seed certification services

A PRODUCING HYBRID SEED The commercial production of hybrid seed involves (*a*) the maintenance and increase of inbred lines (*b*) the production of single cross seed, (*c*) the production of double cross seed and (*d*) processing the hybrid seed [1]

Foundation stocks of inbred lines are maintained by hand pollination to prevent contamination by outcrossing The inbred seed planted for the commercial production of single cross seed is usually increased in an isolated field with open pollination Four separate isolated fields are required to produce the four inbreds needed for one double cross hybrid It is not advisable to use open pollinated inbred seed that is more than two generations removed from controlled poll nation for fear of contamination with foreign pollen Two additional isolated fields are needed for production of single cross seed and one isolated field is needed for production of double cross seed or a total of seven isolated fields in all

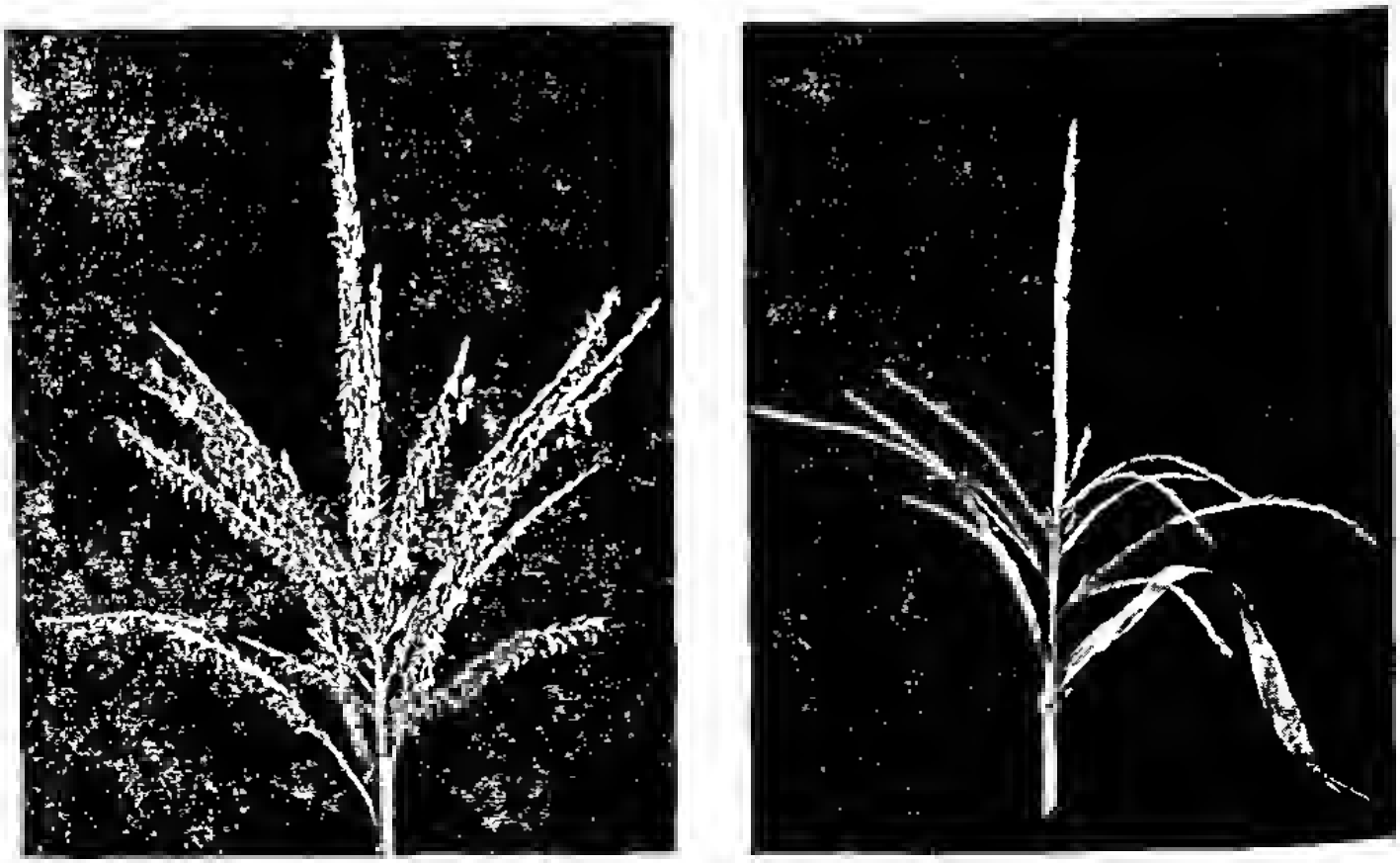
Adequate isolation of seed fields is required to prevent contamination from stray pollen Danger from contamination in single and double cross seed fields is reduced if the male parent is a heavy pollen producer and sheds pollen freely during the period that the female parent is receptive Increasing the number of border rows planted with the pollen parent will reduce the distance needed for isolation Fertile tassels are pulled from the female (ear

Fig 8 11 Detasseling maize The young tassel is removed with a quick jerk care being taken not to injure the maize plant

parent) plants before pollen is shed (Fig 8 11) This requires daily trips through the field during the period of tassel emergence Care must be taken not to pull off leaves along with the tassels since removal of leaves with the tassel will reduce the yield of the plant Normally a ratio of two pollen producing to six seed producing (detasseled) rows are grown in the production of double cross hybrid seed (Fig 8 12)

B USE OF CYTOPLASMIC MALE STERILITY Hybrid maize seed may be produced without detasseling by the utilization of cytoplasmic male sterility (Fig 8 9, 8 13) [15] A maize plant with cytoplasmic male sterility will in the absence of specific restorer genes, produce only male sterile progenies when pollinated by normal fertile maize plants which also lack the restorer genes Fertility is restored

Fig 8 12 A seed production field of hybrid maize Two male, pollen producing rows are grown to six female detasseled rows



8 13A 8 13B

Fig 8 13 A Tassel of male fertile maize plant Note anthers exserted and hanging from staminate flowers B Tassel of male sterile maize plant Cytoplasmic male sterility is used to eliminate detasseling in hybrid seed production

the progeny if the male sterile plant is pollinated by pollen from a plant containing restorer genes An inbred may be converted into a male sterile, providing it does not carry fertility restoring genes, by introducing the chromosomes of the inbred into sterile cytoplasm This is done by crossing the inbred as the pollen parent to a male sterile inbred, followed by repeated backcrossing using the inbred as the recurrent pollen parent, until the genotype of the inbred is recovered in the sterile cytoplasm This will normally require 6 or 7 generations of backcrossing The new male sterile inbred is maintained by pollination from its fertile counterpart Cytoplasmic male sterility has been identified from several sources in maize The most stable and commonly used source was found in the variety Mexican June and is referred to as the Texas type [12 56] The Texas type of male sterility is widely used in the commercial production of hybrids in the U S A Few U S Corn Belt hybrids carry both restorer genes required for this type of cytoplasm so they may be readily converted to male steriles

Fertility is restored to the Texas type of cytoplasm by two dominant genes Rf_1 and Rf_2 [12 14] The gene Rf_2 is present in nearly all forms of maize so that normally only the Rf_1 gene needs to be introduced into an inbred to convert it into a restorer The Rf_1 and Rf_2 genes will give complete fertility restoration in favourable environments However, in certain environments such as high temperature and low humidity, additional modifier restorer genes are required to prevent partial pollen sterility The Rf_1 restorer gene may be added to either a male fertile or a male sterile inbred by successive backcrossing By adding the restorer gene to a sterile inbred, the plants with dominant restorers can be identified following each cross without testcrossing to a male sterile line

Three procedures may be used to utilize cytoplasmic male sterility in production of double cross hybrid maize seed

1. *One inbred male sterile, no dominant restorer genes*

A × *B*		*C* × *D*
Male sterile	Male fertile	Male fertile	Male fertile

AB (Male sterile) × *CD* (Male fertile)

ABCD
Male sterile

The double cross seed (*ABCD*) will be male sterile, since none of the inbreds contain pollen restoring genes A practical way to ensure adequate pollination in the cultivator's field in the absence of pollen-restoring genes is to make an identical double cross, except for the use of male fertile lines throughout, and to blend the male fertile seed with the male sterile seed in the ratio of 1 part fertile to 2 or 3 parts sterile These blends should produce adequate pollen to pollinate all the plants in the cultivator's field

2 *One inbred male sterile, either one or two inbreds with dominant restorer genes*

A × *B*		*C* × *D*
Male sterile	Male fertile	Male fertile	Male fertile (either C or D, or both, with pollen-restoring genes)

AB (Male sterile) × *CD* (Male fertile)

ABCD
50% of plants male fertile if one inbred (either *C* or *D*) contains pollen restoring genes,
or
all plants male fertile if both *C* and *D* contain pollen-restoring genes

3 *Two inbreds male sterile, one inbred with dominant restorer genes*

A × *B*		*C* × *D*
Male sterile	Male fertile	Male sterile	Male fertile (with pollen-restoring genes)

AB (Male sterile) × *CD* (Male fertile)

ABCD
50% of plants male fertile

In each scheme the male sterile inbreds are maintained by pollination from a fertile counterpart.

Detasseling would be eliminated in the production of the *AB* single cross and the *ABCD* double cross in schemes 1 and 2 Detasseling would be eliminated in the production of both single crosses and the double cross in scheme 3

In scheme 2, if we assume the *A* inbred line to have Texas (male sterile) cytoplasm, *B* and *C* inbreds to have normal (male fertile) cytoplasm, and the *D* inbred to have Texas (male sterile) cytoplasm and the dominant fertility restoring gene (Rf_1), we can then represent the cytoplasm and genotypes of the inbreds, single crosses, and double cross as follows

Inbred or cross	Cytoplasm	Fertility restoring genes	Pollen fertility
A-T[a]	male sterile	rf_1rf_1	male sterile
B and *C*	male fertile	rf_1rf_1	male fertile
D TR[b]	male sterile	Rf_1Rf_1	male fertile
AB T	male sterile	rf_1rf_1	male sterile
CD	male fertile	Rf_1rf_1	male fertile
ABCD TR (50%)	male sterile	Rf_1rf_1	male fertile
ABCD-T (50%)	male sterile	rf_1rf_1	male sterile

[a]T represents the presence of Texas cytoplasm

[b]TR represents the presence of Texas cytoplasm and Rf_1 restorer gene

The second fertility restoring gene, Rf_2, is assumed to be dominant (Rf_2Rf_2) in all inbreds in this example, since the Rf_2 gene is present in almost all types of maize, and hence does not usually alter the ratio of fertile and sterile plants in the *ABCD* double cross population

Utilization of male sterility by the commercial grower of hybrid maize seed eliminates the need for much of the labour otherwise required for detasseling, thereby facilitating the production of hybrid seed

c OPEN VS CLOSED PEDIGREE HYBRIDS The pedigree of a double cross hybrid is determined by the inbreds crossed and the order in which they are put together The inbreds used in *open pedigree* hybrids are identified and the pedigree is usually printed on the tag or on the bag of seed Double cross hybrids produced by public institutions are always open pedigree hybrids Most private hybrid maize companies, who have breeding programmes and develop their own hybrids, do not report the pedigree of the hybrids they sell, their identity being considered a trade secret These are referred to as *closed pedigree* hybrids This practice has considerable merchandising value to the commercial hybrid maize seed company The practice may be liable to trade abuse if open pedigree hybrids are secretly coded and sold without accurate identity as to origin In the U S A , by far the major portion of the seed planted is closed pedigree hybrids This has created no problem since the integrity of the major hybrid maize seed producing companies is generally unquestioned

PROCEDURES IN BREEDING IMPROVED MAIZE HYBRIDS

We have discussed what hybrid maize is and how hybrid maize seed is produced We will now turn our attention to how the maize breeder develops improved maize hybrids

Development of Inbred Lines. A maize hybrid is the product of its inbred lines Unless good inbreds are available a good hybrid cannot be developed The first step then in the development of new hybrids, or the improvement of existing hybrids, is to develop superior inbred lines

A SOURCES OF NEW INBREDS Inbreds may originate from *open pollinated varieties, single crosses, double crosses, multiple crosses, top crosses, synthetic varieties* or *germ plasm complexes* In the U S A , open pollinated varieties were the primary source from which inbreds were developed In Mexico, and Central America native open pollinated races of maize have provided a rich source of material for developing inbreds [5 74] In India, the cultivated varieties of open pollinated maize have not yielded good inbreds probably because the original germ plasm introductions were poor and meagre Current southeast Asia maize improvement programmes are based mainly on introduced inbreds from Columbia, Mexico, Cuba, southern U S A , Kenya and other countries As breeding programmes are built up, single, double, and top crosses may be used as sources of inbreds Synthetic varieties and germ plasm complexes may also be fruitful sources of inbred lines In south and southeast Asia, through the combined efforts of the Co ordinated Maize

Improvement Scheme, cooperating breeders in concerned countries, and the maize improvement programmes in India, Mexico and South America, germ plasm complexes are being built up by mixing inbreds and varieties of diverse germ plasm which have potentially good combining ability [11 60] From these germ plasm complexes it is expected that new and superior inbreds may eventually be developed which will fit into hybrids adapted to the various areas of south and southeast Asia

Concern has been expressed frequently that many of the older open pollinated stocks of maize would be lost with the change by the cultivator from open pollinated to hybrid maize This would be a serious loss since the native open pollinated varieties are the principal reservoir of genetic variability in maize It has prompted breeders to retain stocks of seed of open pollinated varieties from many sources In recent years collection, classification, and preservation of native seed stocks from wide areas of Mexico, Central and South America have been undertaken on an extensive scale by plant breeders serving under various auspices (Fig 8 6)[9]

B SELECTION PROCEDURES FOR DEVELOPING NEW INBREDS The procedure for developing inbreds from open pollinated varieties has already been described Selected S_0 (or I_0) plants are hand pollinated and selection is practiced both within and between selfed lines The same proeedure is used to develop inbreds from other sources By use of the backcross, special features such as disease resistance may be added to an otherwise desirable inbred Such a backcross derived inbred would then presumably fit into the same hybrid combination as before and contribute the desirable genes for disease resistance, in addition to the gene complex contained in the original inbred

In any procedure for developing new inbred lines which involves controlled self pollination and selection, the breeder must exercise considerable judgment in (*a*) selecting in each generation the lines that are to be selfed again and carried into the next generation, and (*b*) selecting the plants within the desirable lines that are to be self pollinated In nearly every instance the breeder's selection must be based on the visible characteristics of the plant only Obviously, lines or plants that are diseased, lodged, or unsuited in maturity should not be continued But it is not always obvious which among the superior lines or plants should be carried farther, for often they will be similar in vigour and appearance (Fig 8 14) Various studies have been made to determine whether there are visible plant characters that will be related to the yielding ability an inbred line contributes to its hybrid progeny and that may be used as a basis for selection [18 55 63] In general, these studies show that the more vigorous inbreds tend to give the more vigorous hybrid progenies Other characters which may be used as a basis for selection are maturity, plant height, size of ear, lodging resistance, and disease resistance The more vigorous inbred lines also produce more seed and are easier to maintain

During the period of inbreeding and selection, it is advisable to subject the inbred lines to as many adversities as possible, such as disease, drought, or insect infestation By such tests it is possible to select the lines superior in the characteristics being evaluated

Fig 8 14 Two rows of a uniform, vigorous inbred line.

C PRODUCTION OF HOMOZYGOUS DIPLOIDS In addition to the conventional method of producing inbreds (selection within self fertilized lines), a procedure for developing inbred lines of maize from naturally occurring haploid plants has been suggested [6] It is based on the observation that in some strains about one maize kernel out of each 1,000 will have the haploid chromosome number of 10 instead of the normal diploid chromosome number of 20 (10 pairs) Many of the haploid plants will grow to maturity, and about one out of every ten haploids can be self fertilized successfully to give a homozygous diploid progeny The lines developed from doubled haploids are completely homozygous whereas inbreds developed by the conventional method may never quite reach this state of homozygosity

The essential steps in the production of homozygous diploid plants of maize by this method are as follows

1 Identification of haploid plants in progenies of crosses by the aid of suitable marker genes

2 Growing the haploid plants and self pollinating those that produce viable pollen

3 Establishing homozygous diploid lines (comparable to inbred lines) from progenies of the self fertile haploid plants

Haploid plants have been found in inbred lines, single crosses, double crosses, top crosses, and open pollinated varieties They may be identified by crossing two stocks in which the pollen parent carries a dominant marker gene such as one which produces purple plant colour The haploid seedling plants (about one per thousand which have developed without fertilization by the purple pollen parent) may be easily recognized since they will not exhibit the purple colour These plants are examined cytologically to make sure that they have the haploid chromosome number The haploid plants are then grown to maturity A spontaneous doubling of the chromosomes in a part of the tassel of the haploid plant will result in the formation of viable pollen, and a spontaneous doubling of the chromosomes in a part of the ear shoot will result in the development of viable eggs A simultaneous doubling of the chromosomes in both the anthers and the ear shoot, so that self fertilization may be effected, will occur normally in about one out of ten haploid plants The diploid plants subsequently developed from these self fertilizations are increased and tested in hybrid combinations in the same manner as inbred lines By this method about one to three years may be saved by development of homozygous diploids from an open pollinated variety, or another source, as compared to the time required to develop relatively homozygous lines by inbreeding In the U S A, homozygous diploids are now being used in some commercial maize hybrids

Combining Inbreds into Single and Double Crosses After an inbred is developed, it is crossed with other inbreds and its productiveness in single and double cross combinations is evaluated From experience it has been learned that some inbreds combine with a large number of other inbreds to give high yielding hybrid progenies, certain other inbreds combine satisfactorily with few or no inbreds [16] The ability of an inbred to transmit desirable performance to its hybrid progenies is referred to as its *combining ability* The average performance of a particular inbred in a series of hybrid combinations is known as its *general combining ability* [65] *Specific combining ability* refers to the performance of a combination of two specific inbreds in a particular cross Specific combining ability is judged by the relation of the performance of inbreds in a particular cross to the average performance of the inbreds in a series of crosses [65] For example, if the average yield of the progenies of crosses between inbred *A* and inbreds *B*, *C*, *D*, *E*, and *F* is high, then inbred *A* is said to have good general combining ability If in this series of crosses the yield of the progeny *AB* was considerably below the average, while *AE* was above the average, then the specific combining ability of the *AB* combination would be poor, whereas the *AE* combination would have good specific combining ability

Whether two particular inbreds will combine to produce a high yielding single cross will depend upon the extent to which favourable genes for yield from one inbred supplement those contributed by the second inbred Two inbreds with yield genes which complement each other in this manner are said to "nick" and their single cross progeny will exhibit considerable hybrid vigour Experience has shown that unrelated inbreds derived from diverse germ plasm will generally combine to produce higher-yielding single crosses than inbreds derived from related parent material which might have more of the same genes for yield in common [18]

A TESTING GENERAL COMBINING ABILITY WITH

TOP CROSS TESTS In the beginning, maize breeders systematically crossed the new inbreds they developed and tested the performance of each single and double cross combination This proved to be a laborious task if the number of inbreds was large Later a simpler and less arduous method, the inbred-variety cross, was suggested[26] for the preliminary testing of a large number of inbreds The *inbred-variety* cross, more popularly called the *top cross*, is a testcross between an inbred line and an open-pollinated variety, a single cross, or some other suitable tester strain The series of inbreds to be tested are pollinated with pollen from the common tester strain, either by hand pollination or by open pollination in an isolated field The following season the performance of the top cross progenies are tested in a yield test Only the inbreds with superior top cross progeny performance are retained for further crossing Single or double crosses are now used most commonly as tester strains in top crosses although earlier the open pollinated variety was widely used The top cross test measures the general combining ability of the inbred lines being tested [65]

B TESTING SPECIFIC COMBINING ABILITY WITH SINGLE CROSS YIELD TESTS Inbreds with good general combining ability, as determined by the top cross test, are then grown in single cross yield tests to determine the specific combining ability of particular hybrid combinations The inbreds to be tested are generally combined in all possible single cross combinations The number of single cross combinations that can be made from n number of inbreds may be calculated from the formula $n\,(n-1)/2$ From 10 inbreds it is possible to make 45 different single crosses, or 190 single cross combinations can be made from 20 inbred lines The magnitude of the single cross testing programme soon becomes enormous if a large number of inbreds is to be tested It is for this reason that the top cross test has been adopted as a preliminary test The number of single crosses that will need to be made and tested is thereby greatly reduced

C PREDICTING YIELDS OF DOUBLE CROSSES FROM SINGLE CROSS YIELDS. Since the cultivator usually grows double cross hybrid maize, it is necessary to test the performance of superior single crosses in double cross combinations The number of possible double cross combinations that can be made from n number of inbreds is $3n\,(n-1)\,(n-2)\,(n-3)/24$ With 10 inbreds it is possible to make 630 double cross combinations, or 14,535 double crosses may be made from 20 inbreds From these figures it may be readily visualized that making and testing all of the possible double crosses would be an impossible task if many inbreds were involved

A method for predicting the yield of possible double crosses from the yield of the single crosses[16 21 29] is used widely by maize breeders The average yield of the four "nonparental" single cross combinations is used as the predicted yield for a double cross An example will serve to clarify the method With four inbreds, *A*, *B*, *C*, and *D*, it is possible to make six single cross combinations, $A\times B$, $A\times C$, $A\times D$, $B\times C$, $B\times D$, and $C\times D$, which may be combined into three double cross combinations as follows:

$$(A\times B)\ \times\ (C\times D)$$
$$(A\times C)\ \times\ (B\times D)$$
$$(A\times D)\ \times\ (B\times C)$$

The predicted yield of the double cross combination $(A\times B)\times(C\times D)$ would be the average yield of the four single cross combinations that do not enter into this particular double cross They are $A\times C$, $A\times D$, $B\times C$, and $B\times D$ The actual and predicted yield of the hybrid, U S 13, grown at Columbia, Missouri, is given in Table 8 2 The pedigree of U S 13 is (WF9×38-11)×(Hy×L317)

Table 8.2 Yield of Nonparental Singles, Predicted Yield of Hybrid U S. 13, and Actual Yield of U.S. 13 at Columbia, Missouri

Item	*Yield (bushels/acre)*
nonparental singles	
WF9 × L317	68 7
WF9 × Hy	74 6
38-11 × L317	63 5
38-11 × Hy	76 7
average of nonparental singles (predicted yield of U S 13)	70 9
actual yield of U S 13 in same	

Unpublished data from A
ment Station.

After the double cross yields have been predicted from the single cross yields, the double cross combinations with the best predicted yields are chosen and those double crosses made The double crosses are then grown in yield tests to determine their actual performance in the field in comparison with the best hybrid combinations already in commercial production

SYNTHETIC VARIETIES OF MAIZE

A synthetic variety in maize refers to the open-pollinated increase from a multiple hybrid [16 64] The development of synthetic varieties in maize was suggested as early as 1919 [17] Two advantages have been suggested for synthetics as follows

1 A synthetic might be preferable to a hybrid in low income areas of the world to eliminate the need for cultivators to purchase hybrid seed new each year [62]

2 The greater variability of a synthetic might permit more adjustment than a hybrid to variable growing conditions [34]

Synthetics have been developed which are superior to open-pollinated varieties, but generally they are not as productive as the best double cross adapted to the area The greatest progress has been made in breeding high-yielding synthetics where lines with good combining ability were chosen to enter into the synthetic [34] By using the recurrent selection principle, it is possible to increase further the yield of the synthetic through several selection cycles [37] A synthetic may also be used as a source from which to isolate new and improved inbred lines, or as a pollinator in a top cross test

In the Inter Asian Maize Improvement Programme, several synthetics are being developed, utilizing recurrent selection to improve yield and adaptation These synthetics may be utilized as varieties in underdeveloped areas until hybrids are available and accepted, or they may eventually be used as sources of germ plasm for developing new inbreds [62]

COMPOSITES AND GERM PLASM COMPLEXES

In the Inter Asian Maize Improvement Programme, various composites and germ plasm complexes are being built up as source materials for further breeding work [62] In general the *composites* include various breeding materials put together on the basis of yield potential, maturity, disease resistance, or other known characteristics Usually the seed is mixed and planted at several dates to ensure good cross pollinations between all of the components Selections may be made after 4 or 5 generations at which time innumerable recombinations will be present in the population The term *germ plasm complexes* has been used to designate broad groups of materials mixed together in many ways [11 60] Generally less information will be known about the germ plasm materials included than in the formulation of the composites

OBJECTIVES IN BREEDING HYBRID MAIZE

Choice of the proper objectives is necessary for the maize breeder to develop new hybrids that will be superior to those now in use and that will be adapted to the area where the hybrids are to be grown [67] To be sound, the choice of objectives must be based on a careful appraisal of the characteristics of the maize plant which may be improved and an accurate evaluation of the benefits of such improvements to the cultivator in the production of a crop of maize Improvement in certain features may affect the performance of the maize plant in several ways For example, resistance to the maize borers will decrease the amount of lodging, reduce ear dropping, retard the entrance of disease organism into the stalk, all of which will affect the total yield It is necessary for each breeder to be familiar with the hazards of his particular area, *i e*, what diseases are important and what are the insect pests Then he must concentrate his breeding programme on those objectives that will be most beneficial in his particular area

Yield. Yield is the foremost consideration in the breeding of hybrid maize Potentially, maize is the most productive cereal Maximum yields in maize of 180 quintals/hectare have been recorded as compared to 100 quintals/hectare for wheat The inherent ability of hybrid maize to produce superior yields is the main reason that it replaced the open-pollinated varieties in the large maize growing areas of the world Along with the development of hybrid maize, there were initiated many important studies designed to learn more about the inheritance of yield Some of the theories which purport to explain hybrid vigour have already been discussed Other studies were made to find

the best breeding system by which favourable yield gene combinations might be accumulated into a hybrid All this research, although much of it is theoretical in nature, has as its final goal the breeding of higher-yielding hybrids

Yield is the most complex objective with which the maize breeder works Basically it is determined by the action of numerous genes, many of which affect vital processes within the plant, such as nutrition, photosynthesis, transpiration, translocation, and storage of food materials Yield is also affected directly or indirectly by maturity, lodging resistance, disease and insect resistance, and other characteristics which may be evaluated more accurately than yield by visual selection, and for this reason are generally used as a basis of visual selection in the development of inbred lines. The comparative yields of maize hybrids can be measured only in carefully conducted yield tests grown in the area where the hybrid is adapted Plots are harvested and the weights of the maize are corrected to a constant moisture basis (usually 15 5 per cent) before calculating yields

Adaptation Adaptation, like yield, is a complex objective in the breeding of maize hybrids because it may encompass so many plant characteristics Factors affecting adaptation are (*a*) maturity, (*b*) response to soil fertility level, and (*c*) resistance to heat and drought These are not the only factors influencing adaptation of maize hybrids, as many other plant characteristics, either directly or indirectly, may determine the suitability of a specific hybrid for use in a particular environment For example, the disease or insect resistance of a hybrid may affect its adaptation in certain areas, or the length of the husk covering affects the suitability of a hybrid in areas where insects and birds are serious The latter will be discussed as specific breeding objectives

A MATURITY The time of flowering in maize is influenced by the photoperiod There is considerable difference in the day length (or more accurately the length of the period of darkness when referring to photoperiodic effects on flowering) between north India and Pakistan and south or southeast Asia It cannot be expected that the same varieties may be planted throughout the entire area. In the U S.A extremely early varieties have been developed for the long days of the northern states and late maturing varieties for the southern states Varieties from central and northern U S A perform very poorly when brought to southeast Asia Those introduced from Mexico and Central America where daylenghts more nearly correspond to those of India and southeast Asia have in general performed better than hybrids from the central cornbelt of the U S A While maize is grown as a kharif crop in north India it does better as a rabi crop in south India if irrigation can be provided This further complicates the variety problem, but some varieties do well in either season In general, early maturity is desired so that maize will fit into double cropping systems Selection and testing must be done in the areas where the maize is to be grown to ensure that the hybrid will be of proper maturity Photoperiod insensitive varieties might have a much wider adaptation than photoperiod sensitive varieties

B RESPONSE TO SOIL FERTILITY LEVEL To obtain maximum production of maize it must be grown under high fertility levels This requires that inbreds be selected and hybrids be tested at high fertility levels so new hybrids developed will respond well to fertilizer and yield well at high fertility levels. The maize improvement programme in India used 80 pounds of nitrogen and 60 pounds of P_2O_5 per acre on the breeding nursery at the beginning of the breeding programme This has since been increased to 135 pounds of nitrogen per acre, balanced with P_2O_5 and K_2O [62] It has been found, not only in India but also in Thailand and Indonesia, that as better germ plasm and cultural practices are used, increased responses to higher levels of fertility are obtained

In the USA, there is increasing interest in planting maize in narrow rows to increase plant populations and yield at high fertility levels Early maturing hybrids tend to respond most favourably to this treatment At extremely high plant populations there is often a tendency for many plants to be barren and nonproductive Intensive selection for ear production at high populations may need to be practiced to improve this characteristic

C RESISTANCE TO HEAT AND DROUGHT Injury to maize by heat and drought may occur in many ways The total effect is to reduce yield The degree of yield reduction may be so slight that there is no visible effect upon the plant itself, or it may be so severe that no grain will be produced or the plant may even be killed Either of these environmental

factors may act alone or their effects may be combined to reduce yields of maize Maize grown in the kharif season may not be affected by heat or drought unless its growth extends beyond the period of rainfall and supplemental irrigation cannot be provided or is not provided in sufficient quantity Maize grown in the rabi season may not suffer from heat unless its growth extends into the high temperatures of the summer season Under these conditions seed set may be poor due to failure to produce pollen killing of pollen by high temperatures retarded silking in relation to pollen shedding [68] or drying out of the silk to such an extent that pollen does not germinate [69] Drought damage may occur to maize at any time during the rabi season unless adequate moisture is provided by irrigation

Stress for selection under drought conditions may be provided by withholding irrigation and by increasing the planting rate Selection may be made for (*a*) strains that produce good yields in the presence of drought (*b*) freedom from leaf firing, (*c*) early silking in relation to time of pollen shedding and (*d*) long pollen shedding periods [68] Hybrids with multiple ear tendencies might be useful in areas where occasional droughts occur In seasons with favourable moisture supply more than one ear would develop In seasons when rainfall or irrigation water is deficient only one ear would be formed Earliness in a hybrid may enable it to escape drought damage that comes late in the season

Lodging Resistance Maize hybrids need good lodging resistance if they are to stand and produce high yields with high fertility and adequate soil moisture Losses in yield due to lodging may result from the maize plant falling or breaking over The ears on the lodged stalks may be reduced in size if the lodging occurs early the ear may be lost entirely if it becomes broken off, or the quality of the grain may be reduced if the ear on the lodged stalks touches the ground and becomes damaged

Most hybrids are more resistant to lodging than open pollinated varieties In the development of inbred lines resistance to lodging is always an important basis for selection because differences in lodging are easily observed An inbred with good resistance to lodging will transmit this characteristic to its hybrid progenies In rating inbreds and hybrids for lodging resistance they are commonly scored for (*a*) root lodging and (*b*) stalk breakage (Fig 5 8)

A maize plant is generally classified as *root lodged* when it leans more than 30 degrees from the vertical A strong root system will enable the maize plant to stand up against the buffeting of wind and rain The importance of a strong root system is increased where liberal soil fertility amendments especially nitrogen have been added Root lodging may be caused by (*a*) an inherently weak root system (*b*) rotted roots, or (*c*) roots damaged by insects Inbred strains of maize with the ability to stand erect usually possess larger root systems than do strains inclined to lodge [33] The force required to pull maize plants from the soil has been used to measure the anchorage and the extent of the maize root systems [21] Strains with well developed and healthy root systems require a greater force to pull them from the soil than strains with weak or diseased root systems Strains with short plants and ears set low usually stand better than strains with tall plants and ears set high Much of the progress that has been made in breeding for resistance to lodging has resulted from increased resistance to root rotting diseases [32] Injury to roots by cultivation or by insects provides good avenues for the entrance of disease invading organisms unless the hybrid possesses considerable resistance to these diseases Some of the disease organisms which cause root rots are *Pythium* sp , *Diplodia zeae*, and *Gibberella zeae* [32]

A maize plant is arbitrarily classified as *stalk lodged* if the stalk breaks below the ear Stalk breakage may occur either before or after maturity Inbreds and hybrids show considerable differences in their ability to remain standing without stalk breakage especially after the stalk has matured Several factors may influence the way strains resist stalk breakage These include (*a*) the inherent strength of the stalk, (*b*) the resistance to disease and (*c*) the resistance to insect injury

The toughness of the hard outer shell or rind, as well as the size of the stalk and the strength of the pith, are important in determining its inherent strength Stalk rotting diseases are common causes of stalk lodging with the stalk usually breaking over at the disease infected nodes [32 48] There is considerable variation in the capacity of strains to resist the ravaging of the stalk rotting diseases Damage by maize stalk borers may weaken stalks and

provide entry for the disease-infecting organisms Disease organisms which commonly cause stalk lodging are *D plod a zeae* and *Gibberella zeae*

Resistance to Ear Dropping Resistance to ear dropping is important because ears broken off and dropped on the ground are generally damaged before recovery or lost completely Resistance to ear dropping is usually recorded as the percentage of ears on the ground when harvest is started Hybrids differ in their susceptibility to ear dropping Factors affecting the differences in resistance are (*a*) strength of the shank (*b*) disease resistance and (*c*) insect injury to the shank supporting the ear Resistance to ear dropping is enhanced by selecting for short strong shanks and resistance to stalk and ear rots

Husk Covering The husk protects the maize ear from weather damage and reduces the injury caused by insects and birds A long husk extending well beyond the tip of the ear and remaining tightly closed after maturity is essential to prevent insect and bird injury to the ear (Fig 8 15) Insects entering through the tip of the husk leave tunnels through which ear rotting organisms may enter and add to the damage caused by the insect Hybrids with long husks usually have small ear size In areas where long husks are desirable as in south and southeast Asia varieties with prolific or multiple ear tendency may tend to compensate for the smaller ears The small to medium sized ears of the prolific strains are generally well covered by husks all of which contribute to the adaptation of the hybrid

Disease Resistance Much progress has been made in the U S A Mexico and Central America in breeding disease resistant strains by the simple expedient of selecting for lodging resistance and high yield Inbreds and hybrids that were susceptible to root or stalk diseases would be eliminated from the breeding nursery because they lodged or because their yields were unsatisfactory The importance of disease resistance in maize was fully recognized [9] but the strains of maize usually varied in degree of resistance and did not exhibit a clear cut difference between resistance and susceptibility Many of the maize diseases such as the root stalk and ear rots are inherited in a complex manner rather than by simple single or complementary gene inheritance as is often found with resistance to the rusts and smuts of wheat and other cereals In recent years more attention is being given to the

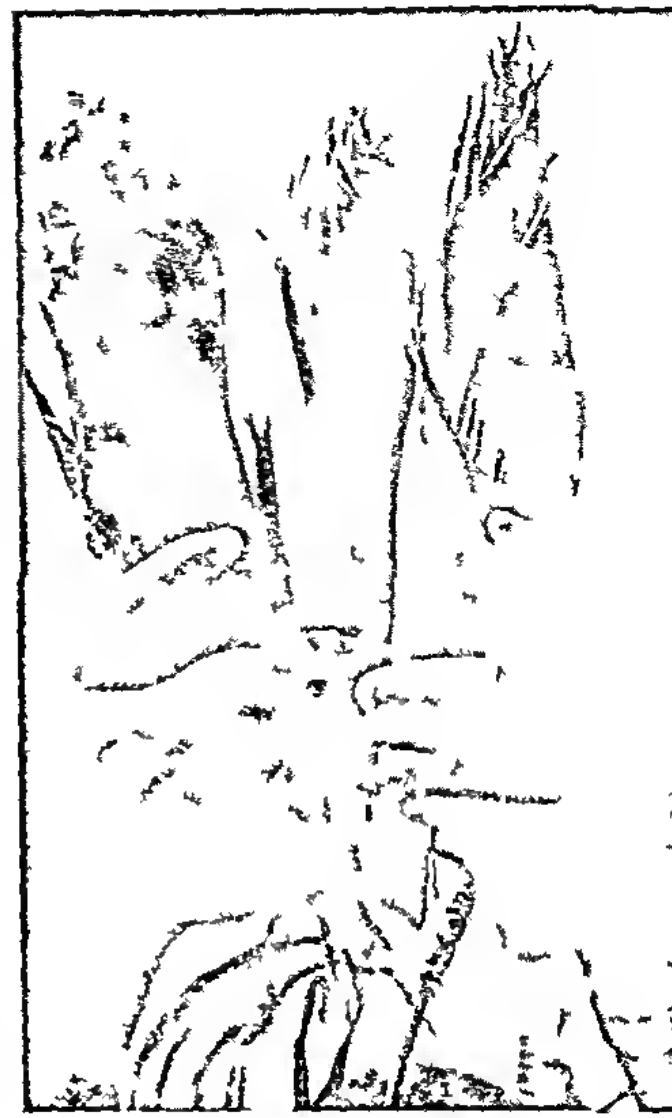


Fig 8 15 Maize ears showing good husk covering

breeding of disease resistant strains This has been accompanied by the development of techniques by which maize may be inoculated with specific disease producing organisms

A SEEDLING DISEASES Seedling diseases may reduce stands by killing or blighting the seedling plants before emergence or soon afterwards Surviving seedlings may be weak or dwarfed with partly rotted roots and sprouts Species of *Pythium*[33] and *Fusarium*[2] are common organisms causing seedling blight. Little is known about the extent of damage to maize in south and southeast Asia from the diseases or sources of resistance In the U S A seedling diseases are common if the maize seed germinates during a period of cold wet weather Resistant strains of maize have been identified by germinating

seed of the different varieties at low temperatures in contact with soil infested with seedling disease producing organisms [22 70]

B ROOT, STALK, AND EAR ROT DISEASES Root diseases weaken the root system of the maize plant and thereby reduce its ability to supply the plant with adequate moisture and plant food as well as to make it likely to lodge Organisms of the *Pythium* species are a common cause of root rotting Various stalk rotting organisms may also invade the plant through root injuries caused by cultivation or insects [32]

Stalk rots cause reduced yields through injury and premature dying and broken stalks Much of the stalk breakage in a maize field is the result of stalks weakened by stalk rotting diseases Common stalk rots caused by fungal diseases and the organism inciting the disease are

Phythium stalk rot, *Pythium butleri* Subr
Diplodia stalk rot, *Diplodia zeae* (Schw) Lev
Gibberella stalk rot *Gibberella zeae* (Schw) Petch
Charcoal rot, *Macrophomina phaseoli* (Maubl) Ashby

These organisms commonly enter the plant through wounds, insect tunnels or other injuries Little is known about the general distribution of these or other stalk rotting diseases in south and southeast Asia, the extent of injury, or sources of resistance [10 48 66]

Several ear rots cause damage to the maize crop [31] The most common organisms causing ear rots are *Diplodia zeae, Fusarium moniliforme, Gibberella zeae*, and *Nigrospora oryzae* The organisms enter the ear through loose husks or insect damage at the tip of the ear or, as in the case of *Diplodia zeae*, may enter through the shank or the base of the husk Various degrees of resistance have been observed in inbreds developed in the U S A but little is known about resistance of inbreds grown in south and southeast Asia to these or other ear rotting fungal diseases

A bacterial stalk and ear rot of maize caused by *Erwinia carotovora*, is causing widespread losses in some areas of India Diseased plants have weakened stalks which may eventually collapse and break [19 50] Distribution and extent of damage is not fully known and little is known about sources of resistance

Techniques for the artificial inoculation of maize with root and stalk rots have been worked out By growing maize seedlings in soil infested with root rotting organisms it is generally possible to differentiate resistant from susceptible lines Stalks of maize may be inoculated with stalk rotting organisms by injecting a spore suspension into the stalk with a hypodermic needle, or by inserting tooth picks (or pipe cleaners) infected with the stalk rotting organism into a hole in the stalk about ten days after pollination Several weeks later, the stalk is split lengthwise and the extent that the disease has spread up and down the stalk is used as the measure of resistance

C LEAF DISEASES Three common *Helminthosporium* leaf spot diseases of maize occur in India The diseases and the casual organism are

Leaf blight (northern leaf blight), *H turcicum*
Leaf spot (southern leaf blight), *H maydis*
Helminthosporium leaf spot, *H carbonum*

Leaf blight produces long greyish green spots on the leaves which increase in number as the intensity of the infection advances Yield losses up to 90 per cent have been reported Leaf spot occurs more in warmer areas of the country than does leaf blight The *Helminthosporium* leaf spot was only recently recorded in India for the first time [4] Intensive studies of the three *Helminthosporium* leaf diseases have been made in the U S A Physiologic races of the organisms have been identified and inoculation techniques worked out in which spore suspensions are sprayed onto the maize plants Different genes for resistance have been identified and resistant inbreds have been developed in the U S A Information is needed on the physiologic specialization of these organisms in southeast Asia A modified recurrent selection programme for resistance to leaf blight has been initiated in India [48] Resistance to the leaf blight and leaf spot diseases appears to be polygenic in inheritance

Rust, incited by *Puccinia sorghi*, infects maize in India particularly in the hill areas [49] Many physiologic forms of *P sorghi* occur in the U S A and resistant varieties of maize have been identified Little is known about the races in India or sources of resistance to them

Brown spot disease of maize, incited by *Physoderma maydis*, is prevalent in some parts of India Circular or irregular brown to purple spots are produced on the maize leaf by the fungus, the development of the spots being favoured by warm

8 16A 8 16B

F g 8 16 Breeding for resistance to maize shoot borer A Young plants are nfested by placing an egg mass nto the leaf whorl B Maize plant showing dead heart which has been k lled by shoot borers feeding n leaf whorl

and humid weather [48] Sources of resistance have not been identified

Downy mildew incited by *Sclerospora phil ppinensis* affects maize in India [45] Symptoms produced are discolouration of foliage and stunting of plants Breeding of resistant strains appears to be the most practical means of control but little information on sources of resistance are known for India and south east Asia

D VIRUS DISEASES Maize mosaic a virus d sease of maize with mosaic symptoms has been reported in India [6] Recent surveys show the disease to be dis tributed over large areas of India The virus is transmitted by several species of aphids Several inbreds from the U S A and Central America have been found to be resistant [47]

Insect Resistance Developing inbreds and hybrids with res stance to insects has been an important phase of breeding maize hybrids in the U S A [41] There hybrids have been developed which show considerable tolerance or resistance to the European corn borer and to ear worms

The most important insect pest of maize in Ind a is the stalk borer *Ch lo zonellus* The young cater pillar feeds on the leaf and subsequently bores into the shoot When the young plant is attacked the growing po nt may be k lled producing what is called a dead heart Infestation techniques have been developed in which eggs or larvae are placed inside the leaf whorl of young plants (Fig 8 16) The larvae feed on the leaves and then bore into the stems causing susceptible types to be injured or killed [7] Seedling plants do not show tolerance or resistance, so insect feeding tests are not made on

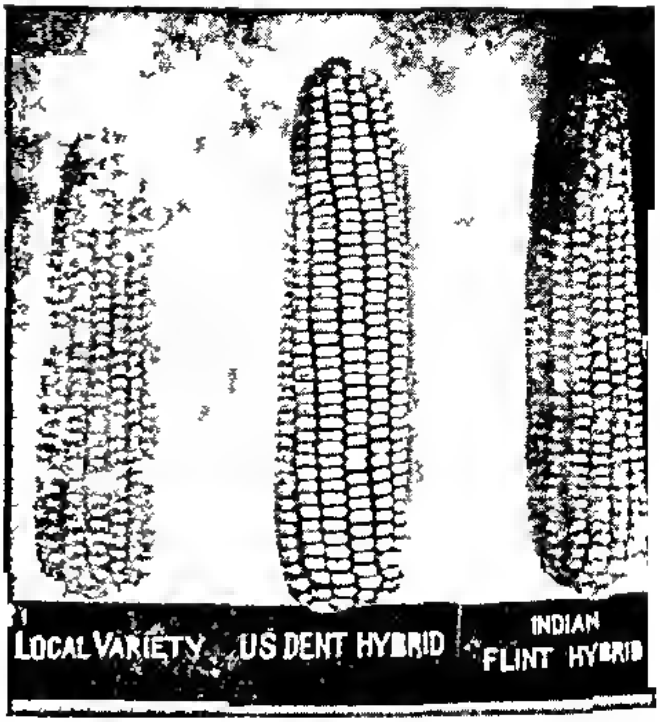
plants less than three weeks of age Inbred lines from U S A and Mexico have shown resistance following artificial infestation in India and are being used in the development of synthetic varieties

Quality Breeding to improve grain quality of maize must take into consideration the use that will be made of the maize In India Pakistan and southeast Asia maize is grown primarily for human food and as the maize acreage increases it may be expected that maize will become increasingly more important in the food habits of the people Maize is also in demand in some areas as poultry feed a use that may be expected to increase Commercial utilization of maize for starch is another use that will require increasingly larger amounts of maize

A FLINTS VS DENTS Flint varieties are preferred to dent types by the people of south and southeast Asia for eating (Fig 8 17) Not only is there a preference for the flavour and texture of the flints but they are also preferred for home grinding The flints have a round seed whereas the seed of the dents are flat and often must be put through the mill two or three times to get a fine grind If dent inbreds are used in a hybrid they need to be masked by crossing with one or more flint inbreds Except for the high starch types hybrids released by the India Coordinated Maize Improvement Scheme have been orange yellow flint types

B BREEDING HIGH PROTEIN MAIZE Breeding for higher protein would increase the nutritional value of the maize The possibility of increasing the protein content of maize by breeding has been demonstrated at the Illinois Agricultural Experiment Station [61 75] Starting in 1896 with Burr White an open pollinated variety of maize with 10 92 per cent protein the protein content after ten generations of selection had been increased to 14 26 per cent (Table 8 1) and after fifty generations of selection it had been increased to 19 45 per cent In contrast a line selected during fifty generations for low protein content had been reduced to 4 91 per cent protein The protein content of a hybrid is increased as the number of high protein inbreds is increased and the final analysis of the hybrid is approximately the average of the inbreds from which it is derived To obtain a high protein content in the hybrids it is necessary to grow them on soils abundantly supplied with nitrogen

Increasing total protein of a hybrid by breeding may not improve the nutritional value of the maize for some classes of livestock Protein in maize is composed of two fractions (*a*) proteins found in the germ which are nutritionally balanced but which comprise only about 20 percent of the total protein in maize and (*b*) proteins found in the endosperm known as *zein* which have inadequate amounts of two essential amino acids *lysine* and *tryptophan* and are therefore nutritionally deficient When total protein content of maize is increased by breeding or by the application of nitrogen fertilizer the zein fraction increases more rapidly than the germ proteins Thus the feeding value of high protein maize to non ruminant animals is not always raised in proportion to the percentage increase in protein quantity in the hybrid



8 17A 8 17B 8 17C

Fig 8 17 Representative ears of A Local maize B US Dent hybrid C Indian flint hybrid

Recently a mutant gene known as *opaque 2* has been identified that changes protein composition or quality by increasing the lysine content of the maize endosperm [41] In a backcross progeny the endosperms from the opaque-2 kernels produced 69 per cent more lysine than the endosperms from normal kernels Identification of the gene became possible by development of refined analytical procedures so that large numbers of maize genotypes

could be analyzed quickly and economically The superior nutritional value of the proteins in opaque-2 maize endosperms has been proven by feeding it to rats which gained in weight an average of 97 grams in 28 days as compared to an average gain of 27 grams for rats fed on standard maize [42] These and similar experiments may have far-reaching effects on improving the nutritional level of man in those areas of the world where cereals form the principal item in the diet

C. HIGH OIL CONTENT The Illinois experiment on breeding for high protein content was accompanied by a study on breeding for high oil content [61 75] The oil content of the original Burr White variety of maize was 4 70 percent This was increased to 7 37 percent after ten generations of selection (see Table 8 1) and to 15 36 percent after fifty generations of selection The line selected for low oil content contained only 1 01 percent oil after fifty generations Most of the oil in maize is in the germ, so selection for strains with large germs will increase the percentage of oil

D SPECIAL PURPOSE HYBRIDS The development of a starch industry in India has led to increase and distribution of two white dent hybrids for starch purposes [46] These crosses are of interest because they are three way crosses involving the cross of a single cross with an open pollinated variety

Attention is being given to the development of sweet or sugary types of maize for India In these types the presence of the sugary gene prevents the conversion of starch to sugar This type of maize is used in the U S A exclusively for home consumption of green ears "Sweet Maize Hybrid No 1" has been produced in India by combining inbred lines selected from crosses between U S sweet types and Indian flint types Popcorn varieties grown in India at present are low yielders Improvement in yield could be obtained by breeding hybrid varieties of popcorn

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9

Breeding Sorghum

The sorghums are native to Africa and Asia where they have been grown for several thousand years India, Burma, and Pakistan are the principal countries in which sorghums are cultivated in south and southeast Asia In India sorghum, locally known as jowar, is the second most important cereal in acreage grown, although in grain production it is third being slightly below wheat as well as rice, the principal cereal Largest acreages are found in peninsular India, the Malwa Plateau and the Punjab region of India and Pakistan [9] The grain of sorghum forms a staple food in the diets of the rural people in these areas and the fodder is fed to livestock Sorghum has generally been grown as a rainfed crop since it will grow on soils of low fertility and withstands drought better than most other cereals Under these conditions of production yields are generally low

In the U S A , where the breeding of sorghums has advanced rapidly, sorghums were introduced from Africa and India during the latter part of the nineteenth and the early part of the twentieth century Sorghum cultivation there increased immensely following the breeding of dwarf early varieties which could be harvested with the combine-harvester Within the past decade the development of hybrid sorghums has further increased the yields and the importance of the crop Early, short stature hybrids from the U S A are now being introduced into India where they are being used as basic breeding materials in the breeding of sorghum hybrids for southeast Asia

CLASSIFICATION OF THE SORGHUMS

Sorghums belong to the family *Gramineae*, and the genus *Sorghum* Most proposed taxonomic classifications have been quite complex and the exact number of species in the genus *Sorghum* has not been settled In an extensive botanical study Snowden described 31 species of the cultivated sorghums,[56] but sorghum breeders usually treat all of the cultivated sorghums as one species, *Sorghum vulgare*

The sorghums are an amazingly diverse group of plants, probably more diverse genetically than any other crop plant They vary tremendously in height, tillering ability, leaf number and size, juiciness of the stalk, seed size and texture, seed coat colour, endosperm colour, size and compactness of the panicles, and a host of other ways With such a diverse group of plant types, it is not surprising that many attempts have been made to classify the sorghums but that none of the systems has met with universal approval

In the U S A the commercial types of sorghum are generally classified according to use as (*a*) grain sorghum, (*b*) sorgos or sweet sorghums, (*c*) grass sorghums, (*d*) broomcorn and special purpose sorghums [25 30 3-] Since sorghums from the U S A are being utilized in the sorghum breeding programmes in India it may be useful to briefly describe these types

Under grain sorghums are included those varieties which have relatively large palatable seeds which thresh free from the glumes, and which are grown primarily for the production of grain The stalks vary from dry to moderately juicy and from no sweetness to slightly sweet according to the particular variety The grain sorghums, all of which are annuals, have been divided into fairly distinct variety groups such as *milo*, *kafir*, *hegari*, *feterita*, *durro*, and *shallu* [61] The *milos* are characterized by a compact head borne on a recurved peduncle and by large and yellow seeds The stalks are slender, dry, pithy and tiller freely The milos have constituted one of the main groups of grain sorghums The *kafirs* have strong stout stalks which are generally juicy and moderately sweet, with cylindrical, erect heads, and medium sized white, pink or red

seeds *Hegari* is abundantly leafed and has moderately sweet juice and seed more chalky in appearance than kafir *Feterita* has compact and erect heads and large, white, chalky seeds *Durros* also have large, white, starchy seeds borne in a compact head *Shallu* has a taller stalk, with small pearly seeds borne in an open panicle

The *sweet sorgos* possess an abundance of sweet juice and are suited for use as silage or fodder, or the juice may be pressed out and used in making syrup Seeds are generally small, coloured, often bitter and unpalatable, and do not thresh clean from the glumes Crosses between the grain and sweet sorghums have produced dual-purpose varieties with both large palatable seed and sweet juice

The *grass sorghums* are grown for pasture or forage Two types of grass sorghum are grown, sudangrass and johnsongrass Both have slender stems, open heads, and vigorous tillering capacity Johnsongrass, which is a perennial and spreads by rhizomes, may become a serious weed pest

The *special purpose* sorghums include miscellaneous types such as broomcorn, waxy sorghums, and pop sorghum types Broomcorn has a long brush used in making brooms Waxy sorghums are grown commercially for a waxy type of starch Pop sorghum pops like popcorn

Many of the Indian sorghums resemble the durros or shallus in the above grouping According to the classification of Snowden, most Indian sorghums would be included in the species, *S cernuum*, *S subglabrescens* and *S durra*, and some semiwild types into *S roxburghii* In general, the Indian sorghums have evolved over many years with specific local adaptation What is most important is that maturity types have been selected which fit into the temperature and rainfall patterns of particular areas Seed colour and quality have been adapted according to local preferences Generally, pearly-white varieties are grown in Maharashtra, Mysore, and Gujarat, chalky whites in Rajasthan, Madhya Pradesh, and parts of Madras, and yellow seeded varieties in parts of Madras and Andhra Pradesh Red seeded varieties are grown also in some local areas Tall growing types have generally been favoured in the past since the fodder is used for cattle feed as well as the grain being utilized for human food

BOTANY OF THE SORGHUMS

The sorghum head varies from a compact to an open panicle The spikelets usually occur in pairs, one being sessile and the second borne on a short pedicel (Fig 9 1), except for the terminal spikelet which is borne on a branch and is accompanied by two pedicelled spikelets [59] The sessile spikelet contains a perfect flower The pedicelled spikelet is usually sterile The sorghum flowers bloom during the night or the early morning Blooming starts in the uppermost panicle branch and follows a fairly regular downward progression From six to nine days are required for all flowers in a panicle to finish blooming [59] The anthers and stigmas push out

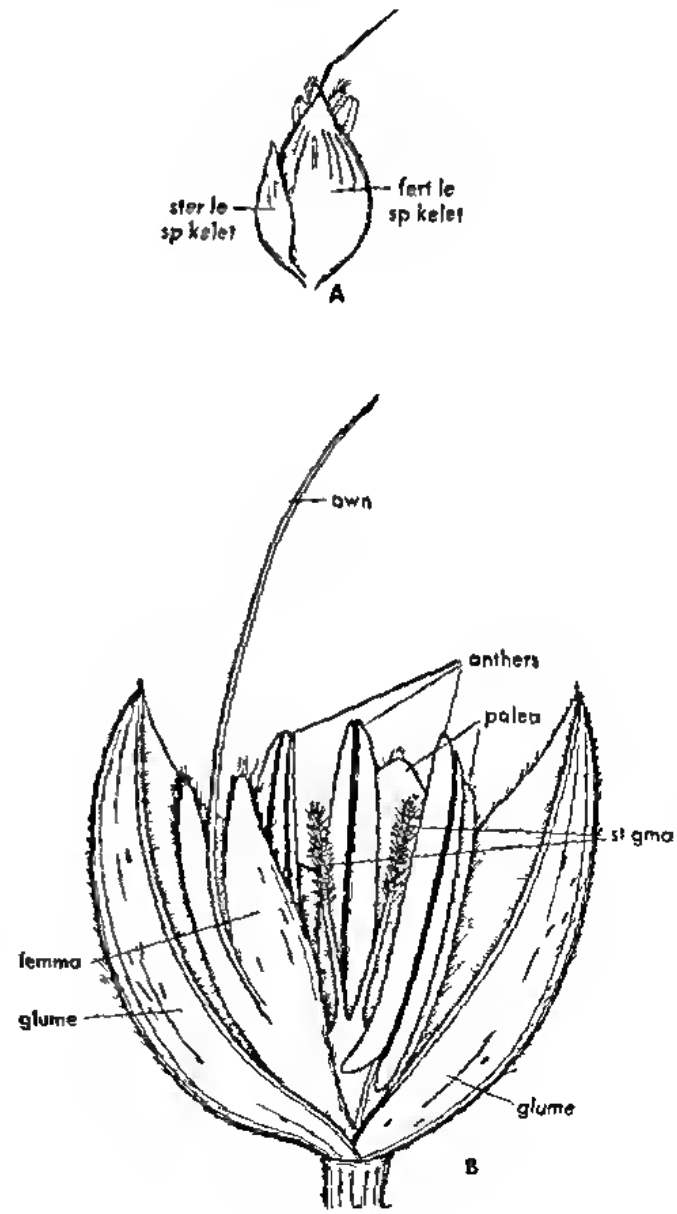


Fig 9 1 Spikelets of sorghum A Pair of spikelets B Fertile spikelet

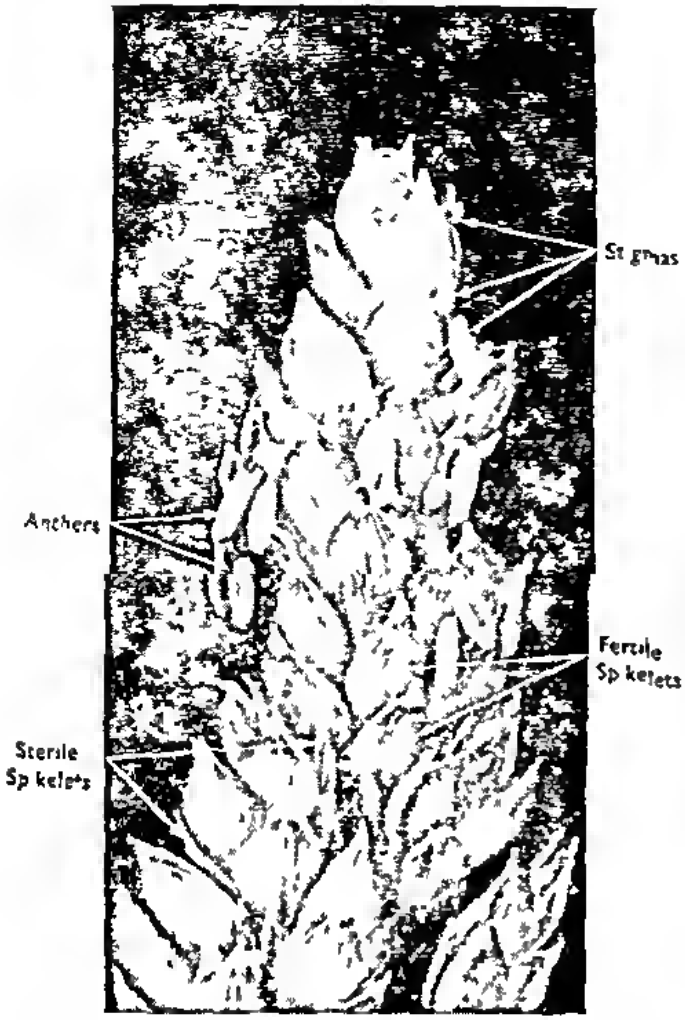


Fig 9.2 Panicle branch from sorghum head. Exposed stigmas and exserted anthers are visible. If the stigma is exposed before being pollinated, cross-pollination is possible. Sorghum is normally about 6 per cent cross-pollinated.

as the glumes open (Fig. 9.2). The anthers dehisce as they are exserted, or shortly thereafter, and release a small cloud of pollen. A single panicle of sorghum may produce from 24 to 100 million pollen grains. The pollen of sorghum loses its viability within a few hours. The stigmas are receptive for one or two days before the flower blooms and for eight to sixteen days after blooming.[2,53]

Stigmas exposed before the anthers dehisce are subject to cross-pollination (Fig. 9.2). The amount of natural cross-pollination in sorghum averages about 6 per cent.[17,23,45] Natural cross-pollination in sudangrass is greater than in other common sorghums. Cross-pollination is greater in varieties with open panicles than in varieties with dense panicles. To control pollination, it is necessary to enclose the sorghum head in bags during the blooming period. Bagged heads of sorghum are frequently injured by insects which hatch inside the bag and eat the sorghum grains. Damage of this type may be prevented by treating the bagged heads or by using bags impregnated with an insecticide.[13]

Artificial cross-pollinations are made by emasculating the seed parent and hand-pollinating it with pollen collected from the pollen parent.[38,45,63] Hand emasculations are made by using fine-pointed tweezers, a dissecting needle, a sharp pencil point, or a small emasculation instrument[19] to remove the anthers (Fig. 9.3). Usually, only a small branch of the panicle is emasculated. Enough of the panicle is clipped away to permit bagging the emasculated head, but too much trimming may have an adverse effect on seed set due to drying out. Pollen is collected in bags in the same manner as with corn and dusted over the exposed stigmas, or the pollen-producing head may be brushed or dusted over

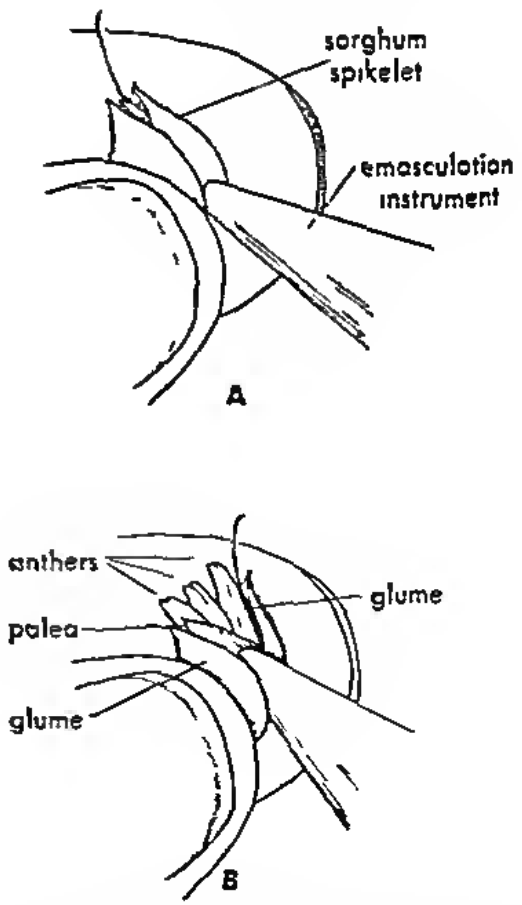


Fig 9.3 Emasculating sorghum flowers. A. Glumes are opened with a medium-sharp lead pencil, tweezers, or emasculation instrument while spikelet is held between the thumb and forefinger. B. Anthers are pushed out by applying pressure through the palea, with a rotating movement.

the emasculated head A mass method of emascula tion has been devised which uses heat to kill the pollen [58] In this method the sorghum head is im-mersed in water heated to a temperature of 48 degrees Centigrade and left for 10 minutes This temperature kills the pollen but not the pistil Some sorghums are more sensitive to heat than others and a slightly lower temperature, 47 to 47 5 degrees Centigrade, may need to be used to avoid injury [45] A modification of this procedure has been suggested which uses plastic bags thereby facilitating more rapid and efficient operation [16] Emasculated heads and heads already pollinated, are enclosed in paper bags to protect them from wind blown pollen Flowers on male sterile plants do not need to be emasculated but must be bagged before natural cross pollination occurs, and may then be pollinated as described above when the stigmas are receptive Both genetic and cytoplasmic male sterility are available in sorghum

Sorghum is a short day plant, and blooming is hastened by short days and long nights However, varieties differ in their photoperiod sensitivity [41] The response of the different varieties to photo-period is genetically controlled, and is important in the geographical adaptation of sorghum varieties

GENETIC STUDIES OF SORGHUM

The cultivated sorghums, *Sorghum vulgare*, have a chromosome number of $2n=20$ Some of the wild, annual, grass like species, such as *S versicolor*, have chromosome numbers of $2n=10$ Other species such as *S halepense* and *S almum* have chromosome num bers of $2n=40$ [6 22] This suggests a basic chromosome number of $n=5$,[7] and that *S vulgare* as well as *S halepense* and *S almum* are polyploids The poly ploid origin has been confirmed by cytological in vestigation [14 18]

A large number of inheritance studies has been made with sorghum [30 45] The inheritance studies of particular interest to the plant breeder are those dealing with seed colour, plant colour, glume colour, maturity, plant stature, juiciness of stalks, sweetness of juice, nature of the endosperm, and disease resistance. Seven linkage groups have been established [45] Three or more genes have been identi-fied in four of these linkage groups, and two genes in the other three linkage groups

Genes Influencing Height. The dwarf varieties of milo presumbly originated as recessive mutants from older and taller varieties Four recessive genes for short stature have been identified [43] The four genes have been designated dw_1, dw_2, dw_3, and dw_4 The genotype, with respect to the four dwarfing genes, in a number of U S varieties is reported in Table 9 1 The effect of the recessive dwarfing genes is to shorten the internode length (Fig 9 4) Time of blooming and leaf size are not affected Tallness is partially dominant One gene assumed to be dw_3, is unstable and reverts to tallness, with one tall mutant plant occurring out of approximately each 1,200 plants [21] The tall plants are not found in varieties which do not have the dw_3 gene The com parative heights under dry land conditions in the U S A of sorghum varieties with different doses of recessive genes are as follows [43]

Recessive for 1 gene	60 to 80 inches tall
Recessive for 2 genes	40 inches tall
Recessive for 3 genes	20 inches tall
Recessive for 4 genes	16 inches tall

Variation in height in individual varieties with the same number of recessive genes indicates the pre sence of a modifying gene complex

Genes Influencing Maturity. Sorghum varie-ties vary considerably in the time required for the plant to develop and mature This variation is important in the adaptation of sorghum varieties to a particular area The length of the vegetative period and the ultimate size of the plant will be determined by the time that elapses before the initiation of the floral bud [40 45] Varieties of sorghum that are slow to initiate the flowering head will have a thick stem and a large number of internodes and leaves, and will be late in flowering and maturity Varieties in which the flowering head is initiated quickly will have a smaller number of internodes and leaves, and will be early in flowering and maturity

In milo, three genes that influence time of maturity have been identified These are designated Ma_1, Ma_2, and Ma_3 [40] Lateness is dominant to earliness but the genes Ma_2 and Ma_3 do not ex-press themselves except in the presence of domi-nant Ma_1, and Ma_3 does not express itself in the presence of Ma_2 As a result only four phenotypes can be recognized from the eight possible homozygous genotypes These are listed in Table 9 2 Ma_3R, an allele to Ma_3 has been found in Ryer milo [44] The Ryer allele is apparently a

Table 9.1 Genetic Classification of Sorghum Varieties for Height[a]

Genetic grouping	*Varieties*
No recessive genes	
Dw_1, Dw_2, Dw_3, Dw_4	none identified
Recessive for one gene	
Dw_1, Dw_2, Dw_3, dw_4	Durra, Tall White Sooner milo, Tall Yellow Sooner milo, Spur feterita, Shallu, Sumac
Dw_1, Dw_2, dw_3, Dw_4	Standard broomcorn
Dw_1, dw_2, Dw_3, Dw_4	none identified
dw_1, Dw_2, Dw_3, Dw_4	none identified
Recessive for two genes	
Dw_1, Dw_2, dw_3, dw_4	Texas Blackhull kafir, Kalo, Early Kalo, Chiltex
Dw_1, dw_2, Dw_3, dw_4	Bonita, Hegari, Early Hegari
dw_1, Dw_2, Dw_3, dw_4	Dwarf Yellow milo, Dwarf White milo, Dwarf Yellow Sooner milo, Dwarf White Sooner milo
Dw_1, dw_2, dw_3, Dw_4	Acme broomcorn, Scarborough Dwarf broomcorn
dw_1, Dw_2, dw_3, Dw_4	Japanese Dwarf broomcorn
dw_1, dw_2, Dw_3, Dw_4	none identified
Recessive for three genes	
Dw_1, dw_2, dw_3, dw_4	none identified
dw_1, Dw_2, dw_3, dw_4	Combine Kafir-60, Day, Martin, Plainsman, Redbine-60, Redbine-66, Westland, Wheatland
$dw_1, dw_2, Dw_3\ dw_4$	Double Dwarf Yellow milo, Double Dwarf Yellow Sooner milo, Double Dwarf White Sooner milo
$dw_2, dw_2, dw_3\ Dw_4$	none identified
Recessive for four genes	
dw_1, dw_2, dw_3, dw_4	no commercial varieties

[a]Adapted from Quinby and Karper [43]

Table 9.2. Genetic Classification of Milos for Maturity[a]

Genetic combinations	*Phenotypes*	*Days from planting to flowering at Chillicothe, Tex.*
Ma, Ma_2, Ma_3	ultra late	92–106
Ma, Ma_2, ma_3	ultra late	92–106
Ma, ma_2, Ma_3	late	76–88
Ma, ma_2, ma_3	intermediate	64–74
ma, Ma_2, Ma_3	early	46–60
ma, Ma_2, ma_3	early	46–60
ma, ma_2, Ma_3	early	46–60
ma, ma_2, ma_3	early	46–60

[a]Adapted from Quinby and Karper[43] and Quinby and Martin [45]

mutant at the Ma_3 locus Ryer milo blooms in 44 days as compared to 50 days for the $ma\ ma_2ma_3$ or $ma\ ma_2ma_3$ genotypes The gene *Ma* is linked with the gene Dw_2 which influences length of the internode

In addition to requiring a greater number of days to reach flowering, the later maturing phenotypes possess a greater number of leaves, greater height, longer leaves, larger stalk diameters, and larger plants than the earlier maturing phenotypes, when grown in normal 14-hour day lengths at Chillicothe, Texas The increased size results from the longer growing period With 10-hour day lengths, the four types cannot be distinguished from one another [42]

Hybrid Vigour in Sorghum Extreme vigour in sorghum hybrids has been demonstrated for many years [3,12,24] Exceptionally tall or vigorous-growing hybrid plants are commonly observed in fields of sorghum and several varieties have apparently originated from this source (Fig 9 5) The increase in grain production in hybrid sorghum comes mainly from greater tillering and an increase in the number of seeds per head [39] Hybrids normally may be expected to exceed the grain yield of the parental means by 25 to 40 per cent where selected hybrid combinations are used [39,60] The magnitude of the vigour, as measured by plant

9 4A 9 4B 9 4C

Fig 9 4 Milo varieties recessive for one two and three genes for height The varieties and their respective genotypes are A Tall White Sooner Milo Dw_1 Dw_2 Dw_3 dw_4 dw_4 B Dwarf White Sooner Milo dw_1 dw_2 Dw_3 Dw_4 dw_4 dw_4 C Double-dwarf White Sooner Milo dw_1 dw_2 dw_3 dw_4 dw_4 dw_4 The Dw_3 gene is dominant in each of these varieties

Fig 9 5 A rogue in a field of dwarf sorghum Tall vigorous hybrid plants or tall mutations are commonly found in commercial sorghum varieties

height, length of the growing season, tillering forage yield and grain yield in several sorghum variety crosses is reported in Table 9 3

The expression of hybrid vigour in sorghum may be somewhat accentuated by the effect of the complementary genes for height and maturity In the first two crosses reported in Table 9 3 the parent varieties have similar genes for height and maturity The superiority of the hybrids over the parents in size, tillering, and yield in these two crosses would thus appear to be a normal expression of heterosis or hybrid vigour, such as that observed in F_1 hybrids of maize or other species, and is unaffected by the complementary action of the height and maturity genes The parent varieties in the last three crosses reported in Table 9 3 possess complementary genes for height and maturity, the influence of which is manifested by the taller and later hybrid plants as compared to the parents The hybrid plants in these three crosses express the combined effect of hybrid vigour and the complementary action of genes for height and maturity The favourable increases in forage and grain yields from heterosis indicate that substantial increases in yield may be obtained in hybrid sorghums and at the same time short stature and early maturity of present varieties may be retained Hybrid vigour accompanied by increases in height or lateness would not be useful to the cultivators who use large amounts of fertilizer or who grow sorghums in tracts requiring short duration varieties

Interspecific Crosses. Interspecific crosses have been made between *Sorghum vulgare* (n=10) and *S halepense* (n=20),[4,18] as well as other sorghum species[8,24] In a cross between Hodo sorgo × johnsongrass,[4] F_1 plants that contained forty somatic chromosomes and that were 85 percent self fertile were obtained The F_2 plants possessed a wide range of the parental characteristics, segregating f height, tillering capacity colour

Table 9. 3. Comparative Vigour of F_1 Hybrid Plants and Parent Varieties of Sorghum[a]

Parent variety	Height (cm)	Growing season (days)	Stalks per plant	Yield per plant (lb)		Increase over highest yielding parent (%)	
				Forage	Grain	Forage	Grain
Crosses between varieties without complementary genes for height and maturity							
PARENTS							
Blackhull kafir	126	105	1 0	0 64	0 20		
Red kafir	126	105	1 0	0 59	0 13		
Spur feterita	157	100	1 3	0 81	0 26		
Sumac	187	100	2 1	1 21	0 26		
HYBRIDS							
Blackhull kafir × Red kafir	135	105	1 7	1 12	0 43	75	115
Spur feterita × Sumac	199	95	2 0	1 40	0 54	16	108
Crosses between varieties with complementary genes for height and maturity							
PARENTS							
Dwarf Yellow milo	143	105	2 8	1 32	0 44		
Hegari	150	125	2 9	1 61	0 36		
Blackhull kafir	126	105	1 0	0 64	0 20		
HYBRIDS							
Dwarf Yellow milo × Hegari	247	136	3 7	3 20	0 79	99	80
Dwarf Yellow milo × Blackhull kafir	277	136	2 8	3 05	0 69	131	57
Blackhull kafir × Hegari	314	153	3 3	4 23	0 88	163	144

[a]Adapted from Karper and Quinby [24]

size, spread of rhizomes, juiciness of stems, and growth habit Three basic types were developed from the segregates, one resembling sorghum, one resembling johnsongrass, and an intermediate type Selections that combine the feed value of the sorghum and the perennial habit of the johnsongrass were found

Polyploidy in Sorghums The sorghum species, *Sorghum versicolor*, *S vulgare*, and *S halepense* have chromosome numbers of $n=5$, $n=10$, and $n=20$, respectively This numerical relationship, as well as cytological evidence,[7 14 18] indicates a polyploid relationship between sorghum species Autopolyploids of the Hegari variety of grain sorghum ($n=10$) have been obtained through the use of colchicine [10] Both tetraploid ($4n=40$) and octaploid ($8n=80$) plants were observed The polyploid plants were shorter, stouter, and flowered later than the corresponding diploids Nineteen per cent of the pollen grains were sterile in the tetraploids and 80 per cent were sterile in the octaploids Unless they can be improved by hybridization and selection, it is doubtful that artificially induced autopolyploids of sorghum will have economic value [53]

Colchicine Induced Variants A new source of true-breeding diploid mutants has been observed in sorghum plants after treatment of seedlings with colchicine [15 52] In one experiment fifteen seedlings from an experimental variety were divided into two groups One group of eight seedlings was left untreated as a check The other group of seven seedlings was treated by smearing a lanolin emulsion containing 0 5 per cent colchicine over the coleoptiles The lanolin emulsion is used to keep the colchicine solution from drying out The eight untreated seedlings grew normally into a uniform group of plants The treated plants behaved quite differently from the untreated Some of the treated

9 6A 9 6B 9 6C 9 6D

Fig 9 6 Variants obtained by seed treatments with colchicine in an experimental line of sorghum from the cross (Dwarf feterita × Dwarf Freed) × Grohoma A Untreated true breeding line from the cross B Variant obtained by treating seed of line A The variant is taller and five to six days earlier than the untreated line C Variant obtained by treating seed of line B This variant is short and three weeks later than the parent line B D Variant obtained by treating seed of line C This variant is taller than parent line C with maturity between line A and line B All plants have a normal diploid chromosome number

plants had more tillers, some differed in stem diameter, or number and size of leaves, some produced greater yields of forage or greater yields of seed (Fig 9 6) Upon selfing some produce uniform progenies and continue to breed true in succeeding generations, others segregate for many characters The exact nature of the colchicine action in producing the true breeding variants is not completely understood It has been suggested that the colchicine induced mutants arise from substitution of chromosomes of similar phylogenetic origin (analogous chromosomes) [52] ' Experimental 3 , a strain which gave rise to many colchicine induced diploid mutants was developed from a 3-way cross involving Day Milo, Black Amber cane, and sudangrass

VARIETIES

Many varieties of sorghum, mostly with local adaptation, have been developed in all of the sorghum producing areas of India as well as in other countries of south and southeast Asia These cannot be enumerated here Recently hybrid sorghums have been developed and released for production in the early and mid duration sorghum areas of India Many more sorghum hybrids will be developed in the future as the Accelerated Hybrid Sorghum breeding project moves ahead The student should consult his Agriculture University or College, or Agricultural Department, for the variety recommendations for his area

ACCELERATED HYBRID SORGHUM PROJECT IN INDIA

The Accelerated Hybrid Sorghum Project was initiated in 1960 to coordinate and intensify the breeding work on sorghum in India The project is being carried out by the Indian Council of Agricultural Research in cooperation with various state research organizations, including some of the new agricultural universities, and the Rockefeller Foundation in India Two lines of study are being concentrated on in the beginning, (*a*) the evaluation of breeding materials, and (*b*) the development of hybrid varieties Two new hybrids, CSH (Coordinated Sorghum Hybrid) No 1 and CSH No 2, were released within the first five years of breeding efforts [50] This is an excellent example of how a well planned and carefully executed breeding programme can function and make rapid progress, if efforts are directed toward the utilization of the best breeding materials and knowledge available

METHODS OF BREEDING SORGHUM

The older methods of breeding sorghum were similar to those used with self pollinated crops, viz introduction, selection, and hybridization Although some cross pollination normally occurs in sorghum, the amount is generally small, averaging about 6 per cent However, self pollination can be assured in the breeding nursery by bagging heads Hybrid sorghums are now grown commercially and most sorghum improvement in the future will undoubtedly involve the breeding of hybrid sorghum

In the past breeding of sorghums in India has been carried out in the states by various state and local experiment stations While good varieties were evolved in some areas, in others the improvement was very meagre The first large scale cooperative breeding effort was the intensive and accelerated programme for hybrid sorghum developed by the Indian Council of Agricultural Research in co operation with various state research organizations With this type of programme rapid progress in breeding hybrid sorghums for the various areas of India has already been made

Introduction and Germ Plasm Collections. The initial step in any breeding programme is to build up germ plasm collections which can be used as a source of breeding materials The germ plasm collections may include indigenous or local types and introductions of exotic strains The Accelerated Hybrid Sorghum Project initiated in 1960 tackled this problem by obtaining the United States Depart ment of Agriculture world collection of sorghum varieties and by adding to it many indigenous strains assembled from collections made in India and elsewhere

The world collection of sorghums was planted in India in the rabi season in 1962 63 at Delhi and Hyderabad and has since been planted several times in both rabi and kharif seasons at several locations Currently around 7,000 different acces sions have been obtained by introduction, ex-change, and systematic collection in India through the Indian Millets Collection Scheme [20] A large number of these accessions are indigenous strains The study of these collections has been made in cooperation with the United States Department of Agriculture and the Rockefeller Foundation Climatic conditions in temperate and subtropical India provide an opportunity for more complete evaluation than could be made in a temperate climate such as that in the U S A , since all of the strains do not flower under the long day conditions at the higher latitudes in the U S A

Cataloging and classification of such a large collection of plant materials is a huge task Not only were observations made on simple botanical characteristics of the plant that will aid in identi fication, but the strains in the collection were eval uated also for such characters as height, maturity, lodging resistance, disease and insect resistance, and grain quality These latter characters are those useful to the plant breeder Eventually the infor mation collected will be assembled and made available to sorghum breeders everywhere Many of the genetic stocks are duplications so that the working collection may be greatly reduced in size

In general, four diverse groups of materials are represented in this huge collection of sorghums each group coming from a different geographic area as follows (*a*) India, Pakistan and South Asia, (*b*) Far East Asia (China, Manchuria, and Japan), (*c*) East and West Africa, and (*d*) U S A [20] Preliminary studies indicate that materials from the different areas will provide sources of breeding mate rial for different characteristics For example, good grain quality for human food and drought and stem borer resistance from the Indian strains, high yield potential, yellow endosperm, and midge resistance from African strains, and high grain yielding poten tial bred for temperate and higher latitudes from the U S materials The genetic diversity in this large sorghum collection will no doubt provide the germ plasm for sorghum improvement for years to come in many areas of the world Perhaps no where has such a vast array of diverse germ plasm for a particular crop been studied with the intensity and thoroughness as is being done by the coopera tive efforts of the Indian and United States plant breeders with the sorghum collection

Selection In earlier days sorghum was treated as a self pollinated crop for breeding purposes and new varieties were evolved by selection of pure lines from local varieties While some protection was needed to prevent cross pollination in the breeding nursery this could be provided easily by bagging heads In India selection was largely for local adaptation and many varieties were developed for almost every different locality and condition in which sorghum was grown It was generally be lieved that local adaptation was so important that varieties could not be moved even short distances and still perform satisfactorily In general, the per formance of the Indian varieties was quite poor, the varieties were tall and lodged easily, and yields were always low The latter was usually expected because sorghum was grown on poor soils with adverse soil moisture conditions

In the U S A the frequent occurrence in sorghum fields of mutant types, or of natural hybrids with increased vigour, led to the selection of many new varieties by both farmers and breeders Successive

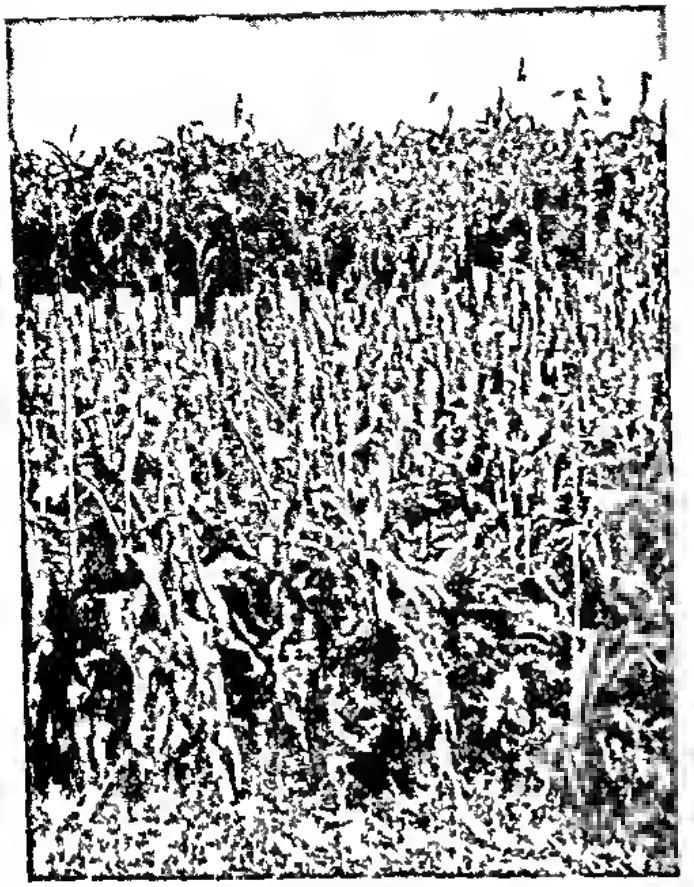


Fig 9 7 Dwarf sorghums from the U S A are being used in the breeding of hybrid sorghums in India Contrast the short, erect, dwarf variety in foreground with the tall Indian varieties in the background

recessive mutations for dwarfness led to the selection of Dwarf and Doubledwarf varieties of yellow milo New varieties with resistance to milo disease were also selected from several older and susceptible varieties [35] Many of these dwarf sorghums are now being used in the improvement of Indian varieties (Fig 9 7)

Mass selection appears to have been seldom used for the breeding of new varieties of sorghum, although it has been recommended as a method for maintaining or improving variety purity This is a natural development since sufficient seed may be obtained from a single head of sorghum to grow a large progeny

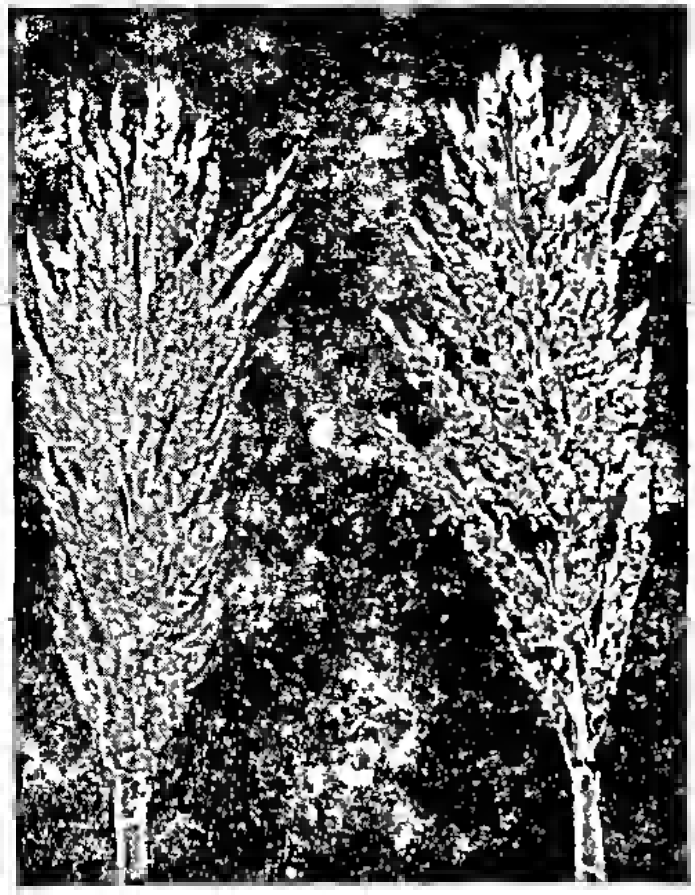
Hybridization. Conventional hybridization procedures were used extensively for originating new varieties of sorghum before the advent of hybrid sorghum [26] In India dual purpose types were developed by hybridization, combining good seed quality with high fodder yield Co 20, a striga resistant variety, has been produced in Madras state by transferring the striga resistance of an African variety to a local type [59]

A progeny-row system of breeding is usually pursued after hybridization The best looking F_2 plants are selected and seed is planted in F_3 rows Selected plants are bagged to prevent natural cross pollination Yield tests begin with the F_4 or the F_5 generation, and lines are increased about the F_6 to F_8 generations Backcrossing has been used in breeding some sorghum varieties Backcrossing is being used in the breeding of hybrid sorghums to add desirable genes, such as those for yellow endosperm, to a parent line Backcrossing may also be used to convert normal lines to male sterility, or to add restorer genes to parent lines in the breeding of sorghum hybrids

Hybrid Sorghums. The success attained with hybrid maize stimulated much interest in the use of this method of breeding with sorghum It had been demonstrated many times that certain sorghum variety crosses produce extremely vigorous hybrids [3 12 24] In this respect sorghum varieties are similar to inbred lines of maize, but unlike maize, inbreeding to develop pure lines in sorghum is not accompanied by a marked visible loss in size and vigour [11] On the other hand, hybrids between selected lines may yield as much as 25 to 40 per cent above the yield of standard commercial varieties [60] For many years the stumbling block to the utilization of sorghum hybrids was the failure to devise an economical means of making the crosses Commercial production of sorghum hybrids finally became possible through the utilization of cytoplasmic male sterility and fertility restoring genes

A CYTOPLASMIC MALE STERILITY In 1950, usable male sterility was found in the progeny of crosses having milo as the female parent and kafir as the pollen parent (Fig 9 8)[57] The male sterility resulted from the introduction of kafir chromosomes into milo cytoplasm When milo was used as the pollen parent, fertility was restored to the male-sterile plants

Numerous varieties of kafir or varieties with kafir parentage then grown commercially in the U S A could be converted to male steriles This was done by crossing the kafir variety onto milo and by backcrossing with kafir as the recurrent and pollen parent until all of the kafir chromosomes had



9 8A

9 8B

Fig 9 8 Cytoplasmic male sterility in sorghum A Male sterile and male fertile heads of sorghum Note exserted anthers on fertile head Both heads are in a similar stage of blooming B Panicle branch from male sterile sorghum head Note exposed stigmas which may be pollinated by wind blown pollen Compare with panicle branch from male fertile head (Fig 9 2) which shows exserted anthers.

been introduced into milo cytoplasm One of the varieties that was converted into a male sterile in this manner was Combine Kafir 60 Pollen fertility in male sterile Combine Kafir 60 (usually referred to as Combine Kafir 60, MS) may be restored by a dominant gene, *Ms*, which was found to be present in a number of commercially grown varieties, mostly milo or milo origin [33] In selecting a variety to use as a pollinator it is necessary that the pollinator variety (*a*) combine with Combine Kafir 60, MS to produce a high yielding single cross hybrid with acceptable grain quality, and (*b*) contain the dominant fertility restoring gene and possible various modifier genes in order to restore fertility and seed production in the F_1 single cross hybrid Numerous commercial varieties were later used to restore fertility to Combine Kafir 60, MS and other lines which were converted to male steriles in the U S A

B PRODUCING HYBRID SORGHUM A scheme for the production of hybrid sorghum seed which utilizes cytoplasmic male sterility is as follows (Fig 9 9)

1 *Developing male steriles* Inbred lines are converted to male sterility by introducing the genes of the line to be sterilized into sterile cytoplasm by a series of backcrosses, using the male sterile line as the female parent and the line to be sterilized as the recurrent and pollen parent Not all lines can be sterilized A new male sterile line must be tested widely to ensure that it remains sterile in a wide range of environments Combine Kafir 60, MS was sterilized by introduction of kafir chromosomes into milo cytoplasm The male sterile strain is designated Strain A The original unsterilized counterpart is strain B

2 *Maintenance and increase of cytoplasmic male sterile strain* Male sterile strain *A* is grown in an

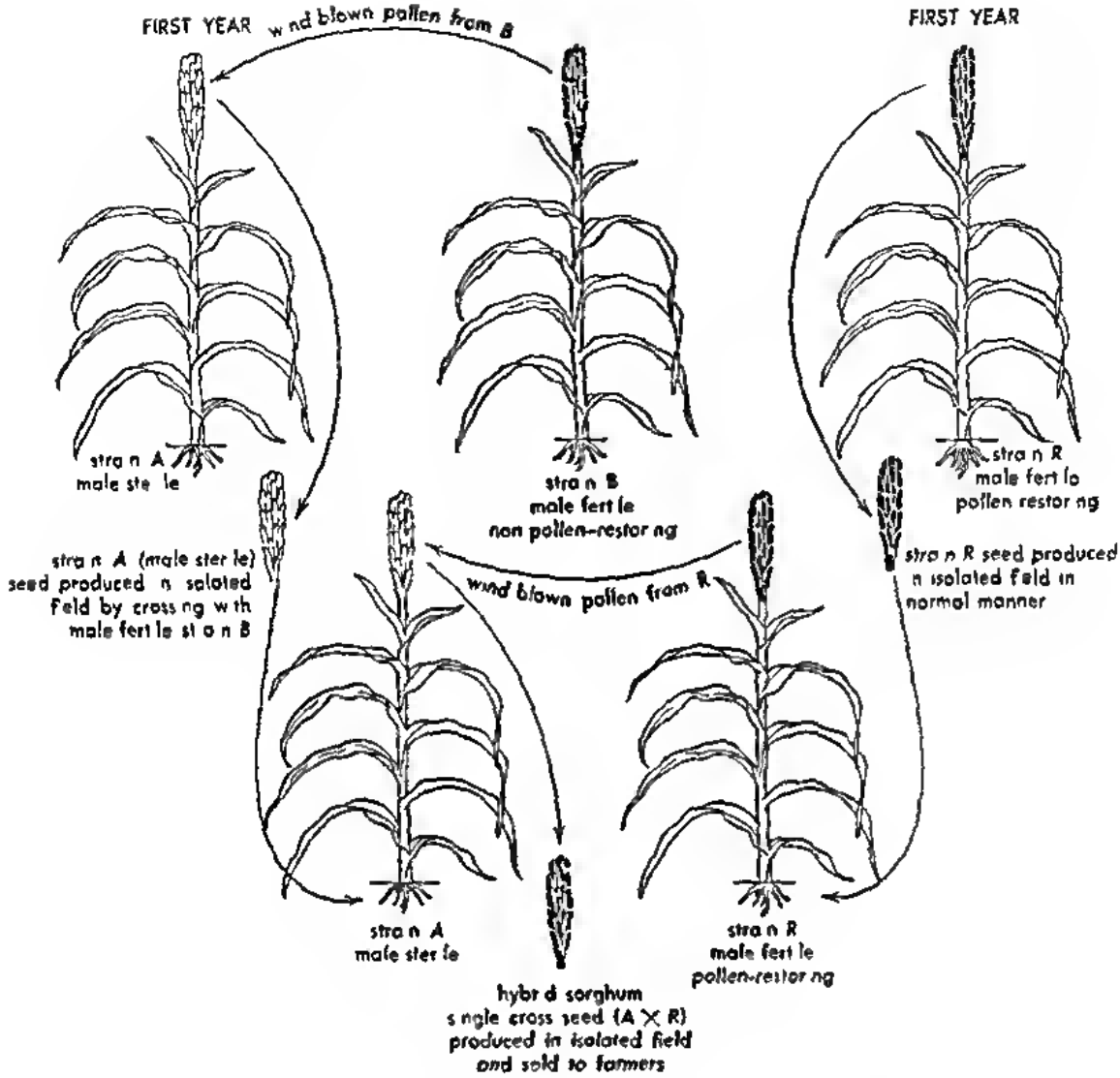


Fig 99 Steps in producing hybrid sorghum seed by utilizing cytoplasmic male sterility

isolated field and pollinated by strain *B* Strain *B* is identical to strain *A* except that it is male fertile

3 *Crossing plot for production of single cross seed* Male sterile strain *A* is grown in a second isolated field and pollinated by strain *R* Strain *R* is unrelated, male fertile, and possesses pollen restoring genes

4 *Utilization of single cross seed* Single cross hybrid seed (*A*×*R*) is grown by the cultivators for commercial producing of hybrid sorghum

The cytoplasm and restorer genes present in the parent lines and the hybrid may be summarized as follows

Material	*Nature of cytoplasm*	*Pollen restoring genes*[a]	*Pollen fertility*
Strain *A*	male sterile	$ms_c ms_c$	male sterile
Strain *B*	male fertile	$ms_c ms_c$	male fertile
Strain *R*	male fertile	$Ms_c Ms_c$	male fertile
Hybrid, *A*×*R*	male sterile	$Ms_c ms_c$	male fertile

[a]Gene symbolization from Schertz and Stephens [44]

In the above example a single pollen restoring gene (Ms_c) is postulated. It is probable that in some

Fig 9 10 Seed production field of hybrid sorghum CHS No 1 Six rows of the female line Combine Kafir 60 MS are at left Two rows of the pollinator IS 84 are at right

cytoplasmic sterility systems modifying genes may be required also as has been demonstrated in wheat and corn The gene symbolization used here contains the subscript letter *c* to identify the cytoplasmic genic male sterility system with which the pollen restoring gene is associated and to distinguish it from gene symbols (*ms*) identifying genetic male sterility systems only

The cytoplasmic male sterility has provided a satisfactory tool for producing hybrid sorghum The parent stocks are easy to maintain, and only three isolated blocks are required to produce the hybrid seed [45]

In the commercial production of hybrid sorghum seed, six rows of the male sterile parent are planted to two rows of the pollinator parent or ratios of 12 4 are also used (Fig 9 10) To ensure a pollen supply over a longer period, it may be advisable to plant alternate pollinator rows on successive dates

The fact that commercial varieties such as Combine Kafir 60 could be converted and used as the male sterile parent in a cross, while other commercially grown varieties could be used as pollinators, reduced the time necessary to get hybrid sorghum into commercial production in the U S A It was unnecessary to self and develop inbred lines first, as was necessary with maize Cytoplasmic male sterility has since been introduced into various Indian strains of sorghum [49]

B *HYBRID SORGHUMS IN INDIA* In 1961 an accelerated hybrid sorghum breeding programme was initiated in India In order to make rapid progress two important decisions were made (*a*) to adopt Combine Kafir 60, MS as the common female parent variety in all immediate crosses, and (*b*) to test a wide range of germ plasms as pollinator varieties The choice of Combine Kafir 60, MS was based on information indicating that the male sterility in it is stable, that it has high combining ability, that it is insensitive to day length and may be grown in both kharif and rabi seasons, that it was of short stature with good lodging resistance and that it has white corneous seeds [46] It was later found to be resistant in India to stem borers Some of the disadvantages to the use of Combine Kafir 60, MS has been its susceptibility to shoot fly, the presence of black glumes which stain the seeds in humid weather, and the presence of latent factors for brown seed coat which in crosses with red and brown seeded varieties gives brown seeded hybrids With Combine Kafir 60, MS as the female parent the choice of pollinators was therefore limited to (*a*) varieties with white pearly or yellow endosperms which would cross with Combine Kafir 60 to produce good seed quality in the hybrid and (*b*) varieties which would restore fertility to the Combine Kafir 60 MS single cross hybrid plants

About 100 crosses were made in 1961 between Combine Kafir 60, MS and white pearly or yellow endosperm varieties gleaned from the large sorghum collection Yield trials of the hybrids were conducted throughout India in 1962 By 1965 two sorghum hybrids had already been released, CSH (Coordinated Sorghum Hybrid) No 1 (Fig 9 11) and CSH No 2

CSH No 1 is an early to medium maturity hybrid with creamy white seeds It is the single cross between Combine Kafir 60, MS and a yellow endosperm selection of feterita Grain yields in extensive tests were 50 to 60 percent above yields of local strains

CSH No 2 is an early to medium maturity hybrid, medium tall in height, with white pearly seeds Grain yields were 60 to 80 percent above yields of local strains It is a single cross between Combine Kafir 60, MS and a yellow endosperm selection of hegari

Release of two hybrids in such a short time is a remarkable accomplishment and is the result of (*a*) careful planning and utilization of knowledge already available, (*b*) fortunate selection of parent materials, and (*c*) a widespread, coordinated

Fig 9 11 CSH (Co-ordinated Sorghum Hybrid) No 1 and parent lines

testing programme throughout India which made it possible to obtain extensive information on the performance of the new hybrids under a wide range of environmental conditions in a relatively short period of testing

OBJECTIVES IN BREEDING SORGHUM

Sorghum grain is used as food for human consumption and the fodder is used for livestock The sorghums are grown over wide areas of India and Pakistan generally under different soil and climatic conditions They are grown mainly in kharif or monsoon season but are also grown in some areas as rabi or winter crops and as spring or hot weather crops. Although grown largely as rainfed crops, some sorghums are grown also with irrigation This presents the breeder with a wide range of uses and growing conditions which must be considered in developing breeding objectives for sorghum While sorghum varieties have generally been considered to have only limited local adaptation in India the experience with hybrid sorghums would indicate that a hybrid may have rather wide adaptation if the proper germ plasms are combined Objectives to be considered here in the breeding of sorghum are yield, maturity, resistance to lodging, disease resistance, insect resistance, and quality

Yield. Sorghums, like maize, have a potential for high productivity of both grain and fodder Productivity of sorghums in India has been very low with an average grain yield of around 500 kilos/hectare Much of the acreage is planted on soils with low fertility and inadequate moisture supply Under such unfavourable conditions cultural practices are also usually poor In tests under more favourable conditions, with heavy fertilization and adequate moisture, yields of 5,000 kilos/hectare have been obtained from some of the new hybrid strains[20] In the U S A sorghum hybrids are producing high yields when fertility and moisture conditions are favourable It is possible then to develop hybrids with high potential productivity if suitable germ plasm combinations are obtained

The growth and yield of a sorghum variety is influenced by inherent plant characteristics such as maturity, height, [illegible] od

by environmental factors such as rainfall, temperature, and day length, and by the interaction of the genotype with the environment In addition to potential yielding ability production of a variety may be affected by inherent varietal resistance to adverse conditions such as drought disease and insects All must be considered in the development of breeding objectives

Maturity Maturity or duration represents length of the period from planting until the variety is mature and ready for harvest Varieties with different maturities are grown in different areas of India Most sorghum is grown in the kharif season as a rainfed crop The variety grown in a particular area then depends upon the length of the period of rainfall and the retention of soil moisture If the rainfall period is long and the soil retains the soil moisture for a long period after the close of the rainy period a late maturing variety will be grown If the rainy period is short or the soil dries out quickly an earlier variety will be grown In the rabi season or in summer irrigated tracts, only varieties of short duration will be grown On the basis of this adjustment to the rainfall and soil moisture pattern the following maturity groupings may be made [20]

late kharif	(130 to 170 days)
medium kharif	(100 to 130 days)
early kharif	(90 to 100 days)
early rabi	(90 to 100 days)
early summer	(90 to 100 days)

Initial breeding work with hybrids has been in the development of hybrids for medium and early maturity areas Hybrid strains may be evaluated for maturity by noting the number of days to maturity, as above, or by the number of days to flowering

The length of the photoperiod (period of darkness) also affects the variety adaptation [21] In general the practice of selecting photoperiod insensitive types has made it possible to grow varieties at different latitudes without appreciably affecting the length of the maturity period and to grow the same variety in both kharif and rabi seasons Specific genes influencing time of maturity have been identified for sorghums grown in the U S A It is not known whether the genes influencing the adaptation of sorghums in India to the different maturity areas are the same genes as those identified in sorghum varieties grown in the U S A

Fig 9 12 Stalks of native Indian sorghum varieties tied together to prevent lodging New dwarf lodging resistant hybrids produce higher grain yield than the tall native types

Resistance to Lodging Most Indian varieties of sorghums are tall and weak stemmed (Fig 9 12) Since the fodder is valuable to the cultivator for livestock feed, the taller and more leafy types have been favoured in the selection of new varieties With heavy winds the tall, weak varieties break over and lodge severely The lodging is increased when sorghums are grown with irrigation or heavy fertilization practices required for obtaining high yields In the U S A, short stiff varieties with one or two dwarfing genes are now grown almost exclusively for grain production These short varieties have the advantage there that they stand until harvested with a combine harvester They can also be grown with heavy applications of commercial fertilizer and with irrigation

One of the considerations in the selection of Combine Kafir 60 MS as a female parent line in initial crosses to produce hybrid sorghums in India was its stout stalks and lodging resistance. While taller than some of the combine types of sorghum grown in the U S A it is much shorter than Indian varieties Hybrids obtained with Combine Kafir 60 MS as a parent are much improved over Indian varieties in lodging resistance Some loss in fodder may follow the use of shorter,

stiffer varieties of sorghum in India This loss can generally be made up by the thicker stands and increased growth following fertilization Lodging resistance *may also be increased by selecting* for resistance to root and stalk rots and resistance to stem borers

Disease Resistance The sorghum crop is affected by several diseases These are described in an ICAR monograph [47] Among those most important in India are leaf blight downy mildew rust sugary disease and the parasitic plant striga Research on breeding for disease resistance in sorghums is just beginning in India

A LEAF SPOT DISEASES Leaf blight caused by *Helminthosporium turcicum* often causes severe damage to sorghum in India [47 61] Seedlings may be killed or stunted and leaves become blotched and dry up prematurely The disease is carried over on the seed or in the soil This is the same disease that causes leaf blight on maize Several varieties were found to be resistant in the USA including two varieties of sudangrass Tift sudangrass was developed from the cross (sudangrass × Leoti sorgo) × sudangrss [6] Only one of 30 000 F_2 plants from this cross possessed the resistance of the Leoti sorgo and the plant characters of sudangrass (Fig 9 13)

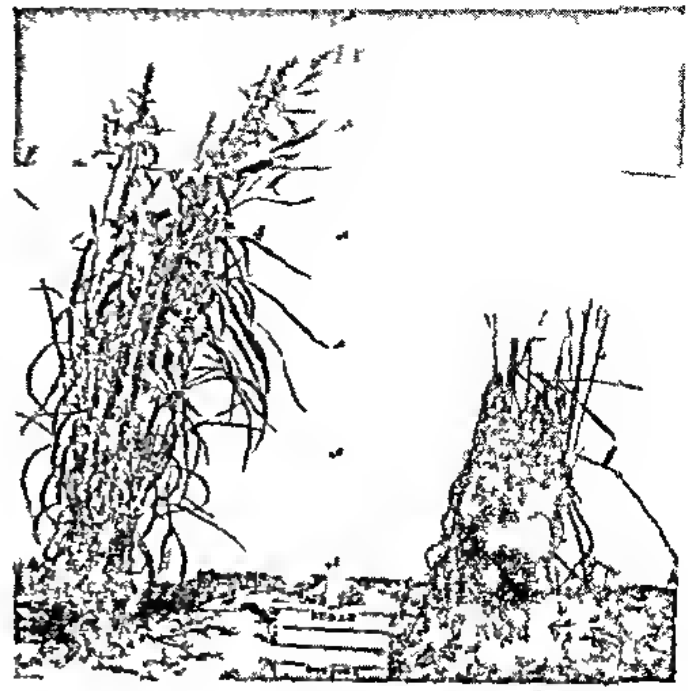


Fig 9 13 *Disease resistant* F_3 plant from cross (Sudangrass × Leoti sorgo) × Sudangrass compared with plant of common Sudangrass which is infected with foliage diseases This is the only plant out of 30 000 F_3 plants examined at the Georgia Coastal Plain Experiment Station Tifton Georgia in 1938 that possessed the disease resistance of the Leoti sorgo parent and the vegetative characters of Sudangrass The Tift variety of Sudangrass originated from this plant

Zonate leaf spot caused by *Gloeocercospora sorghi* produces distinct zonate spots with alternating dark and light bands [47] Infection is more severe in rainy seasons The world collection of sorghums is being searched in India for sources of resistance

Anthracnose and red rot are two phases of the same disease caused by *Colletotrichum graminicolum* [5 47 61] The disease causes tan reddish or purple spots on the leaves and also causes root rot and stalk rot Several varieties of sorgo hegari and pink kafir are resistant to the leaf spotting phase of the disease [28] Tift sudangrss is moderately resistant [6] The red rot or stalk rotting phase is initiated by the fungus invading the crown of the plant spreading up inside the stalk and interrupting the translocation of water and food materials The diseased tissue becomes red with reddish brown or purplish spots on the stalk Lodging of infected stalks is severe Leoti Red and Atlas varieties of sorgo and several varieties of kafir and hegari are resistant Little is known about resistance to varieties in India [47] There appears to be no close relationship between resistance to the anthracnose and red rot phases [27] Artificial inoculation for red rot is made by introducing a spore suspension of the causal organism into the stalk about midway up between time of heading and flowering

B DOWNY MILDEW Downy mildew incited by *Sclerospora sorghi* is common on sorghum in India [47 61] Infected seedlings have pale yellow leaves covered with white fungal growth On older plants the leaves turn yellow or brown and become shredded Dwarfing or stunting may occur as the internodes are shortened and the leaves come out close together Inoculations have been made by covering seeds with oospores or powdered leaves containing oospores Bonita Kasturible and Co 6 varieties were not infected when artificially inoculated in Mysore state [51]

C RUST Sorghum rust caused by *Puccinia purpurea* is a common disease of sorghum [47 61] Early infection may cause severe yield reductions Milos are generally resistant Tests for resistance have been conducted at the Millets Breeding Station Combatore

D SUGARY DISEASE Ergot or sugary disease, caused by *Sphacelia sorghi*, is widespread in India [47,61] In south India the disease is prevalent in the rabi crop and grain formation may be greatly reduced Sweet drops of "honey dew" develop and infected spikelets become a mass of soft fungal growth Hegari and Dwarf yellow milo are resistant Little information is known about resistance of Indian varieties

E ROTS Charcoal rot, caused by *Macrophomina phaseoli*, has been found in rabi crops in some states [47 61] The pith of affected stalks is destroyed by this disease with the result that severely damaged plants are badly lodged Most milos and milo derivatives are severely damaged [29] Feterita, hegari, and sudangrass are moderately susceptible Kafirs and sorgo are more resistant Several varieties of sorgo, Atlas African millet, and Sumac 1712, are resistant [65]

Milo disease, caused by *Periconia circinata*, attacks susceptible varieties of milo and varieties of milo origin [61] Sorghum plants infected with milo disease show 'firing" at five to six weeks of age, a symptom that is difficult to distinguish from drought [30] The leaves roll and develop a yellowish tinge at the margin The plants become stunted and produce poor grain, or die completely After the organism becomes established in the soil, the intensity of the infection builds up with the production of two or three successive crops of a susceptible variety Milo disease is one of the most devastating diseases of sorghum, and without the development of resistant varieties, large scale production of milo could not have been continued in many areas of the U S A Breeding for resistance proved to be relatively easy In disease infested fields, disease free plants could usually be found Selection of these disease free plants often led to the development of resistant varieties The technique of screening for resistance to milo disease is simple Milo selections, or progenies of milo crosses, are grown in infested fields or in greenhouse flats filled with infested soil (Fig 5 9) The resistant plants are easily distinguished from the susceptible plants by their normal appearance Resistance to milo disease is inherited by a single gene with resistance partially dominant [5] It has been suggested that some of the resistant plants found occasionally in susceptible varieties may have arisen by mutation

F SMUTS Several smut diseases are found on sorghums [61] The principal smuts and the causal organisms are covered smut, *Sphacelotheca sorghi*, loose smut, *S cruenta*, and head smut, *S reiliana*

Covered smut causes heavy losses of grain in several states in India [47] The disease is seedborne Several physiological races have been identified in the U S A [29,34] Spur feterita is resistant to all races Additional races have been reported in India [62]

Loose smut also occurs in several states in India.[47] Both grain and fodder yields are reduced by this disease Three physiologic races have been identified in the U S A [29 34] Spur feterita is resistant to all races

The head smut of sorghum destroys the entire head Its occurrence in India is sporadic [47] Feterita and white milo are highly resistant [29]

Sorghums may be inoculated with covered or loose kernel smuts by dusting dry spores over the seed

G STRIGA *Striga* is a parasitic plant that infects the roots of sorghum and other plants from which they obtain most of their food requirements [47 61] Two species, *Striga asiatica* and *S densiflora*, have been reported as causing heavy damage in southeast Asia Early infection will cause stunting of the sorghum plant or even killing of the plant before flowering Varietal resistance would provide a means of preventing loss from this parasite Co 20, a variety released in Madras State, is reported to be resistant [55] Co 20 originated from a cross of a local variety and a resistant variety, Bonganhilo, introduced from Africa

Insect Resistance. Breeding for resistance to insect pests has received much attention in the U S A [37] Two insect pests are receiving attention in the sorghum breeding programme in India These are the stem borer and the stem or shoot fly [29]

A STEM BORER The stem borer, *Chilo zonellus*, deposits eggs in masses on the underside of the leaf After hatching, the larvae feeds in the leaf whorl where they may cause the central shoot to be killed Screening of sorghum varieties for resistance to stem borer is in progress Evidence is encouraging that borer tolerance may be found in Indian varieties

B STEM FLY The stem fly, *Atherigona indica* deposits eggs individually on the underside of the leaves The young larvae feed on the stem, cutting through and killing the main shoot and producing a "dead heart" Young plants may be killed (Fig 9 14) Older plants may produce tillers

Fig 9 14 Plants of exotic sorghum varieties which were planted in the foreground have been largely killed by the sorghum stem fly, *Atherigona indica* while plants of native Indian varieties planted in the background have largely survived

which mature later than the main crop and are reduced in yield Varieties differ in the percent of "dead hearts" caused by the stem fly Some Indian varieties, Co 1 and M 35-1, have had low percentages of "dead hearts "[28]

Quality. The use of the sorghum crop must be considered in breeding for quality The principal use of the grain is for human food while the fodder is fed to livestock

A SEED QUALITY The sorghum seed is used for making chapatis and bread or rotti In general a pearly white grain type with a bright lustre is desired Dark coloured seed coats would give a dark colour to the flour and would be undesirable The seed should also be free of tannin or other astringent substances sometimes found in small amounts in brown or dark-coloured seed coats The latter type seed coats have been favoured in some areas as they impart a certain amount of bird or weather resistance to the grain Dark coloured glumes which contain red, purplish, or black water soluble pigments which stain the seed in humid weather should also be avoided

Sorghum hybrids in India using Combine Kafir 60, MS as one parent are generally inferior in quality for making bread or rotti than the best local varieties which have pearly white grain When male sterile lines with the white pearly type seed are produced and used in crosses, hybrid sorghums will be equal to other types in quality Quality of bread may be judged by such characters as (*a*) appearance, (*b*) texture, (*c*) puffing, and (*d*) taste

Development of yellow-endosperm hybrids which have a higher content of carotene and xanthophyll would increase the nutritional value of the hybrid Some educational work may need to accompany the introduction of such hybrids in order to get full acceptance of the cultivator and use in areas where white pearly types have been grown and are now preferred

Procedures and techniques have not been worked out for precise quality evaluation tests In one experiment eight hybrids were cooked by steaming, boiling, frying, and par-boiling [20] Taste tests were made on the eight varieties with each method of

cooking One hybrid was selected as superior by all methods of evaluation This study indicates that hybrids can be developed with excellent quality characteristics if proper means of screening and evaluation can be provided

B FODDER Most sorghum fodder is fed to livestock The quantity of fodder produced is usually important to the cultivator Short, dwarf types are often frowned upon if the yield of fodder is reduced The total yield and quality of fodder may be increased by thick spacing of the crop and thus compensate for the loss from reduced height Quality of fodder may also be improved by selecting for leafy types, hybrids resistant to leaf diseases, and for sweet juicy stalks with a higher percentage of sweet juice

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10

Breeding Millets

BAJRA (Cumbu Pearl Millet, Cattail Millet)

Bajra originated in Africa from where it was imported into India in the early days [17] It is an important cereal crop in Africa India Pakistan and southeastern Asia but in the USA and Europe it is grown chiefly as a fodder crop

Among the cereal crops in India bajra is fourth in acreage behind rice, sorghum and wheat, and fifth in production behind rice wheat sorghum and maize Like sorghum bajra is generally grown on poor land and in areas of scanty rainfall so that yields tend to be very low Bajra is a food crop of the poorer people and is seldom eaten by those who can afford a choice of foods It is the most drought tolerant of the cereals and a staple food grain in the areas of arid coarse textured soils The grain of bajra is richer in nutritive value than the grain of sorghum but the fodder is inferior in feeding value In India it is cultivated most extensively in Maharashtra Rajasthan Madras, Andhra Pradesh, Uttar Pradesh and Punjab The breeding and improvement of bajra often was neglected because it was considered a low value crop Recently, hybrid bajra has been developed in India and introduced into cultivation (Fig 10 1)

ORIGIN AND CLASSIFICATION

Africa is considered to be the centre of origin of bajra by Stapf,[25] who divides the genus *Pennisetum* into six sections Of 32 species described by Stapf in the section *Penicillaria,* only two are known outside of Africa, *Pennisetum typhoides,* bajra, and *P purpureum,* napier or elephant grass *P typhoides* is a cultivated annual and *P purpureum* is a wild perennial which spreads by rhizomes In a study of the variability of a large number of strains of bajra from Africa and India, the greatest range of variability was found in the strains from Africa [1] This is further evidence of the African origin of bajra since the greatest range of genetic variability in a species is usually found in the areas in which the species originated

VARIETIES

No good classification of the bajra crop has been worked out in spite of the fact that a wide range of variability exists Characters most commonly used in describing varieties include length diameter and compactness of spike, presence or absence of awns

Fig 10 1 Dr D S Athwal former bajra breeder at Punjab Agricultural University, examines spikes of a new hybrid bajra developed in India

or bristles, colour and size of grain, and maturity Many local varieties of bajra are grown These include late, medium and early types the late types are commonly grown in the kharif and the early types in the rabi season Varieties of bajra, like those of open pollinated maize, are extremely heterozygous and show a considerable range of genetic variability as a result of cross fertilization The first hybrid variety, Hybrid Bajra 1 was distributed from the Punjab Agricultural University in 1965 [3] With the accelerated programme of millet improvement that has recently been initiated in India it may be expected that many new hybrids will be developed in the future adapted to the different areas and climatic patterns of India and other countries in south and southeast Asia The student will need to consult his agriculture department or extension service, or the Agricultural College or Agricultural University in his area to learn the recommended varieties

BOTANY OF BAJRA

Bajra belongs to the species *Pennisetum typhoides* Stapf and H H The diploid chromosome number in the species is $2n=14$ The plant of bajra is an annual which may reach a height of several metres Branches may arise from the nodes, each branch terminating in an inflorescence Tillers arise from the basal nodes The inflorescence is a cylindrical spike, tapering toward the ends, and may vary in length from a few centimetres to over a metre (Fig 10 2) It is densely packed with groups of spikelets which vary in number from 2 to 5 with 2 the most common number Two types of flowers are borne in the spikelets bisexual and staminate A characteristic feature of bajra is the subtending bristles, usually 30 to 40 in number, surrounding the spikelet group

Each spikelet contains two flowers partly protected by the glumes The lower flower is usually male and the upper one perfect or bisexual The male flower consists of a single lemma and three stamens, but does not have either a palea or lodicules The perfect flower has a broad lemma thin palea, three stamens, and a carpel with two styles terminating in brushlike stigmas The styles begin to appear 2 to 3 days after emergence of the spike, attaining full length after 36 to 48 hours [12] They remain receptive for 1 to 2 days The anthers emerge after the styles dry up, the anthers of the bisexual

Fig 10 2 A flowering spike of bajra Note that the anthers are exserted in the upper two-thirds of the spike In the lower one-third stigmas are exposed but anthers have not yet been exserted The latter results in a high percentage of cross pollination in bajra

flowers appearing 2 to 3 days before those of the staminate flowers Maximum flowering occurs between 10 00 P M and midnight but anthesis goes on throughout the day The number of spikelets may vary from 800 to 3,000 per spike with an average of around 1,600 [18]

Cross pollination is the rule with about 80 per cent of the flowers being naturally cross pollinated The various lines of bajra vary in their self fertility, some lines are highly self fertile while others are largely self sterile and can be inbred only with difficulty To ensure selfing, spikes may be bagged before emergence of the stigmas (Fig 10 3) As the spike elongates it may be necessary to adjust the bag to cover the lowermost spikelets Another procedure is to enclose within the bag two full spikes from the same plant, one a few days older than the other and ready to shed pollen as the stigmas are emerging from the younger spike [19] Usually, spikes in several stages of anthesis can be found on a plant at the same time

Emasculation in bajra is laborious and difficult due to the small size of the flowers and the late development of the anthers in relation to the stigma However, the interval between appearance

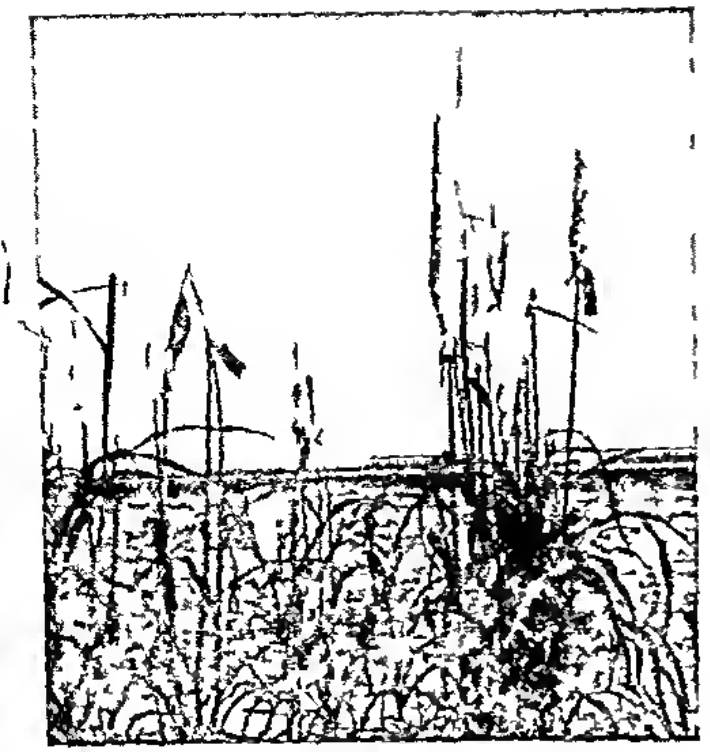

Fig 10 3 Spikes of bajra that have been bagged to prevent natural cross-pollination

of the styles and anthers can be used to advantage for artificial cross pollination The interval is greatest in the lower most regions of the spike (Fig 10 2) About four fifths of the upper portion of the spike is removed and the rest bagged before the styles appear to prevent cross pollination by insects As the styles become receptive pollinations can be made with little chance of selfing since the stamens will not be ripe. Pollen is shed freely and can always be collected in bags enclosing the spikes Flowers are pollinated by dusting them with fresh pollen from the desired male parent plant, or by shaking a spike which is shedding pollen over the exposed styles

GENETIC STUDIES

Genetic studies with bajra have been very meagre Characters which have been studied include chlorophyll deficiencies, leaf characters, panicle characters, bristle characters, and plant pigmentation Many of these are qualitative characters of little interest to the plant breeder Xenia effect of golden yellow grain of an African variety on a spike of an Indian variety with bluish green grain colour has been reported [**] Xenia may sometimes result in bolder grains on a spike It has been suggested that this phenomenon be used in separating hybrid seeds from selfed seeds

Pennisetum typhoides is a diploid species ($2n=14$) with the genome formula *AA* *P purpureum*, Napier grass, is thought to be an allotetraploid ($2n=28$) with the genome formula *AABB* [13] The *B* genome is not homologous with the *A* genome and exercises an overdominance effect An autotriploid ($2n=21$) has been found in the progeny of a sterile diploid ($2n=14$) plant, and an autotetraploid ($4n=28$) has also been produced from bajra following colchicine treatment of seedling plants [20] Interspecific crosses of pearl millet with Napier grass have been made in India and the U S A [6] and selections from the crosses utilized as fodder plants

METHODS OF BREEDING

The large amount of cross pollination in bajra results in the bajra plants being highly heterozygous In this respect a field of bajra is much like a field of open pollinated maize and considerable genetic variability will be found within a single open pollinated variety Breeding methods will therefore follow closely those that have been used with the maize crop The finding of cytoplasmic male sterility in bajra has permitted utilization of hybrid vigour and the breeding of bajra hybrids

Introduction and Germ Plasm Collections. It has already been pointed out that maximum variability in bajra is found in lines collected from Africa where the bajra crop originated The initial step in a breeding programme would be the collection of as many strains as possible, both indigenous and exotic In recent years the Indian Agricultural Research Institute, the Indian Council of Agricultural Research and the Rockefeller Foundation in India collaborated on systematically building up a germ plasm collection of bajras in India This collection now has about 2,000 strains, over half of which came from India and the remainder from Africa, U S A and other countries This collection is being carefully studied and classified to find the materials in it that may be of use to plant breeders

In the past some of the African varieties have been introduced into India for cultivation Jamnagar Giant and Improved Ghana are varieties that have been developed by selection from African introductions [11 13] Other introductions have been hybridized with local strains An outcross of an

African introduction with long bristles resulted in the development of the variety S 530, which inherited long bristles from its African parentage [4] A male sterile line, Tift 23A, introduced from the U S A, is being utilized in the production of hybrid bajra [9]

Selection. Most bajra varieties in India were developed by selection from local types [11] Both mass selection and single plant selection have been used

A MASS SELECTION In mass selection desired plants are selected under open pollination and the seed planted *en masse* This procedure has no doubt been used by the cultivators in maintaining their varieties Mass selection was unquestionably a factor in the evolutionary development of the bajra plant both in Africa and India and has been the method used in the development of many local varieties

B SINGLE PLANT SELECTION Many varieties of bajra are reported to have been developed by single plant selection in Madras, Andhra Pradesh, Punjab and other states [13] Selection of single plants in a cross fertilized crop normally results in mild inbreeding and is sometimes followed by a loss of yield and vigour The fact that varieties could be developed from single plant selections apparently indicates that some lines of bajra can tolerate a limited amount of inbreeding without adverse effects It is also probable that in many cases the selected plant produced seed from open pollination which has the effect of broadening the gene base in the potential variety

C PURE LINE SELECTION Pure line selection to create homozygous inbred lines has been carried out with bajra The procedure is not different from that in maize Pollination must be controlled by bagging spikes to ensure that selfing occurs Like maize, vigour declines with selfing and many defective types are uncovered and may be eliminated during the inbreeding process [15] Many male sterile types will be lost due to their failure to produce pollen [8] Stability in economic characters is usually achieved about the I_8 to I_{10} generation The utilization of pure line selection to produce inbred lines will be accelerated with increased emphasis on the production of hybrid bajra

D RECURRENT SELECTION No published reports are available regarding the utilization of recurrent selection practices in bajra breeding However, recurrent selection would be a useful procedure to concentrate genes for particular characters within an open pollinated population Recurrent selection is being used in the U S A to concentrate yield genes in a male pollinator to be used on Tift 23A *

Hybridization. The variety AF 3 has been produced by crossing African types with local types S 53 was derived from a natural outcross of a local and an African variety Hybridization to obtain genetic recombination in open pollinated types u which parental plants are heterozygous and posses different genotypes, requires different procedure. for selection following hybridization than following hybridization in self pollinated crops in order to prevent loss of vigour with inbreeding In one case a system of crossing within lines and between lines, was followed, the derived "group-bred populations being maintained by controlled mass pollination [13]

Synthetic Varieties. Development of synthet c varieties offers an opportunity to improve the bajra crop Synthetics, as in maize, are the open polli nated progenies of crosses between two or more inbred lines With the increase in the efforts to develop inbred lines, it is possible that inbreds could be combined into synthetics which would be im proved over the present local varieties Synthetics may be useful in low income areas as it would not be necessary for the cultivator to purchase new seed each year In Madras state, synthetics were made by (*a*) mixing seed of 6 inbred lines in equal proportions and (*b*) mixing seed of the 15 possible single crosses between the 6 inbreds [8] Grain yields reported in pounds per acre for three succes sive generations by the two methods were as follows

Method *a* Syn 1, 650, Syn 2, 625, Syn 3, 588
Method *b* Syn 1, 588, Syn 2, 588, Syn 3, 538

From these results it would appear that synthetics could be prepared by either procedure and grown without appreciable loss in yield for at least three generations In Georgia, U S A, Starr Millet [13] a synthetic variety, has been widely grown for forage production Starr Millet yields about 25 per cent more forage during the grazing season than common millet

Utilization of Hybrid Vigour. Utilization of hybrid vigour by the development of bajra hybrids

* Burton Glen W, Georgia Agricultural Experiment Station Tifton Georgia, U S A Personal Communica tion 1966

offers considerable hope for the improvement of the yield of the bajra crop Production of hybrid bajra has become practical since finding cytoplasmic male sterility and fertility restoring genes in the bajra crop The procedure in producing hybrid bajra is similar to that utilized in the production of sorghum hybrids

Before cytoplasmic male sterility was available attention was given in Madras state and in the former Bombay state to the possibilities of utilizing hybrid vigour [10 23] Inbreds were developed, combining ability of inbreds was assessed by top cross tests, and the best combiners mated in single crosses A number of superior hybrid combinations were evolved While such hybrids could be produced experimentally, there was no way to control pollination so that the hybrid seed could be produced economically In 1948 a procedure was suggested for producing hybrid seed by mixing the parent inbreds in a 1 1 ratio and growing the crop under open pollination [7] The seed produced in this way would be a mixture of crossed seed, sibbed seed, and selfed seed When planted at a high rate the crossed seeds in the mixture, with their superior hybrid vigour and competitive ability, would crowd out the selfed seeds so that the remaining stand would largely contain hybrid plants The hybrid, Gahi 1 (Georgia Hybrid No 1), was released in the U S A for production of hybrid bajra by this method Gahi 1 is a fodder variety of pearl millet and four inbred lines were used in its pedigree Gahi 1 has yielded about 50 per cent more fodder than the common millet it replaced

A CYTOPLASMIC STERILITY Cytoplasmic sterility has been reported in bajra from several sources [12 15 21] Burton, working in the U S A , crossed inbred lines used in Gahi 1 with an inbred from Starr millet to increase the leafiness of the former [8] A few male sterile plants were found in the cross with inbred 23 and it was later determined that the sterility was cytoplasmic in nature When the male sterile 23 line, now known as Tift 23A,[9] was crossed with a collection of 41 inbreds representing a wide range of genetic materials, it was found that 27 of the inbreds carried genes for fertility restoration Recently, a cytoplasmic male sterile line has been isolated at Punjab Agricultural University, Ludhiana, from different parent materials This line, L 101 A, has bold seeds and early maturity The Ludhiana line, L 101-A, requires different fertility restoring genes than Tift 23A from the U S A Inbred lines that failed to restore fertility to Tift 23A generally restored fertility to L 101 A This would indicate that cytoplasm restorer gene systems other than that associated with Tift 23A may be developed in bajra

B HYBRID BAJRA The procedure for producing hybrid bajra is essentially the same as that for producing hybrid sorghum (Fig 10 4) The steps are as follows

1 Cytoplasmic sterility is introduced into an inbred line by repeated backcrossing, using a cytoplasmic sterile line as the female and the selected inbred as the recurrent male parent The recovered male sterile inbred is called Strain A The male fertile counterpart is Strain B

2 Strain A (male sterile) is maintained by crossing with Strain B Strain B (male fertile, non-pollen restoring) is maintained by self or sib-pollination

3 Strain A (male sterile) is crossed with Strain R (male fertile and pollen restoring) to produce hybrid bajra seed The seed produced from the A × R single cross will be male fertile and is sold to the cultivator for growing hybrid bajra

C HYBRID BAJRA IN INDIA Following the plan used so successfully for starting a hybrid sorghum programme in India, it was decided to utilize two U S A produced cytoplasmic male sterile lines, Tift 23 A and Tift 18-A as female parents to initiate a hybrid bajra improvement programme [5] To these male sterile inbreds would be crossed the best inbreds that could be assembled from all over India (Fig 10 5) The fact that three crops could be grown in one year in south India, one in kharif, one in rabi, and one in summer, facilitated the rapid crossing of inbreds to the male steriles and the testing of the single cross hybrids After two years of testing the first bajra hybrid, hybrid Bajra No 1, was released in 1965 [3] Hybrid Bajra No 1 is from the cross Tift 23 A MS × *Bil* 3B *Bil* (bajra inbred line) 3B was isolated from the variety, S 350, at the Punjab Agricultural University

In the nomenclature used for designating inbred lines, Tift 23 A MS represents the male sterile A strain The male fertile B strain is designated Tift 23 B Bil 3B, which is the male fertile pollinator in the above cross, is the R strain Bil 3B contains fertility restoring genes which restores pollen fertility to the F_1 hybrid grown by the cultivator.

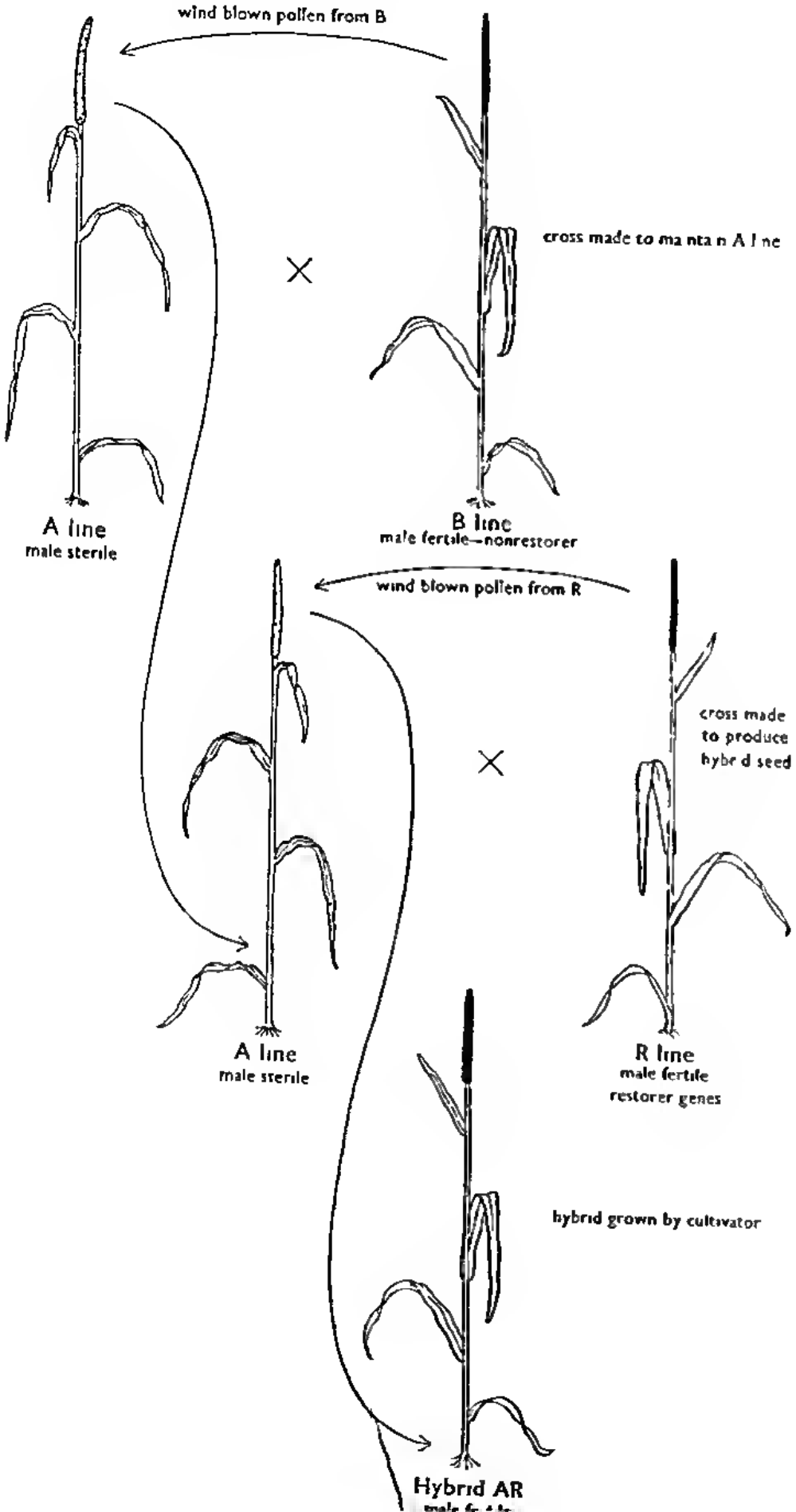

Fig 10 4 Scheme for producing hybrid bajra by utilizing cytoplasmic male sterility The procedure is similar to that used in producing hybrid sorghum

Fig 10 5. Two hybrid bajras produced by crossing Indian lines onto Tifton 18-A MS

BREEDING OBJECTIVES

High yield, early maturity, lodging resistance disease and insect resistance, long bristles, and seed quality are the primary objectives in breeding bajra

Yield. Although bajra, like sorghum and maize, has a very high yield potential, the yield in India Pakistan, and other Asian countries is extremely low, averaging only about 350 kilos/hectare in India The low yield is to a considerable extent due to the practice of planting bajra on soils too poor or too dry to grow good crops of other cereals Selection and testing for new varieties has been done mostly at a relatively low level of fertility Until the programme of breeding hybrid bajra was started recently, little attention was given to testing selections on high fertility levels where the full yield potential of a strain could be expressed Vigour of growth and high capacity for tillering and branching are all expressions of yielding ability Dwarf types that will grow at high fertility levels without lodging are also essential In addition to assembling the best combination of yield genes into a bajra variety or hybrid it is also necessary to obtain resistance to drought, lodging, and disease and insect pests to prevent losses from these maladies

Grain yield potential is greatly improved in hybrid bajra as compared to the older varieties developed by mass and pure line selection In 1964, Hybrid Bajra No 1 yielded an average of 88 per cent more than the best open pollinated varieties with which it was compared at a number of locations in India

Maturity. Bajra is a short duration crop It is usually grown in areas with short moisture supply and needs to mature before the supply of available moisture is exhausted Thus early maturity helps to escape drought damage Early maturity also fits bajra into double cropping systems where a short duration crop with high grain yield potential is needed, either at the end of the kharif season to grow with available moisture, or during the rabi or summer seasons to be grown where supplemental irrigation is available Photoperiod insensitivity will permit utilization of a hybrid in both kharif and rabi seasons Uniformity of flowering within a spike, or among different spikes on the same plant, to facilitate uniform ripening and harvest is desirable Delay in harvesting to permit late set seeds or spikes to ripen may result in considerable bird damage to the early ripened spikes within the field.

Lodging Resistance. Lodging resistance is attained by breeding for short, stout stalks with good thickness of rind and freedom from insects or diseases damaging and weakening the stalk Strong, well developed root systems are also needed to provide good anchorage into the soil The heights of bajra strains vary greatly, but the potential breeding materials for dwarf or semidwarf types are available (Fig 10 6) The Bil 1 inbred line used in Bajra Hybrid No 1 is semidwarf Since the bajra plant is also used for fodder there is always some reluctance on the part of the cultivator to

Fig 10 6 A dwarf bajra variety (Compare in height with bajra in Figures 10 1 10 5 and 10 7)

grow short types However, dwarf and semidwarf types may be selected which have the same number of leaves as the taller types, only the internodes are shortened By thick planting and heavy fertilization fodder yields of short varieties may equal those of taller varieties High grain yield cannot be obtained without heavy fertilization which in turn requires development of shorter types than those that have been grown in the past

Disease and Insect Resistance. The principal diseases of bajra are rust, downy mildew or green ear, and smut Very little work has been done toward breeding for disease resistance Bajra is relatively free of insect pests and little work has been done on breeding for insect resistance (Fig 10 7)

A RUST Rust on bajra is incited by *Puccinia penisetii* It is prevalent in all states in India where bajra is cultivated [24] It may occur during the early life of the plant, drying up the leaves and reducing yields Brinjal and other species of *Solanum* are alternate hosts to the rust organism. Most varieties are susceptible although the strain, No 814/3, was resistant at Coimbatore

B DOWNY MILDEW Downy mildew or green ear, caused by *Sclerospora graminicola*, is prevalent in all bajra growing states in India [24] The symptoms are loss of colour in leaves of young plants, discolouration and streaking of older leaves, and distortion of lateral shoots The ear is transformed into a group of small, green, leaf like structures to which the term 'green ear" is applied Physiologic specialization has been reported Most varieties of bajra cultivated in India are susceptible K 1, a selection from the Kullan variety, was reported resistant in Madras state F_1 hybrids on Tift 23A have also been observed to be resistant

C SMUT Smut, caused by *Tolyposporium penicillariae*, is prevalent in bajra in most states [24] Scattered grains throughout the spike may be diseased, with 1 to 30 percent of the plants infected Indian varieties are generally susceptible although late flowering varieties which flower during the dry season may escape infection No information is available regarding resistant varieties

Long Bristles. It has been observed that long bristles on bajra offer considerable protection to the crop against damage from birds The bristles are hairy outgrowths at the base of the spikelet A new variety of bajra with bristled ears was recently developed at the Punjab Agricultural University from an outcross of local strain with a long bristled introduction from Africa [4]

Quality. The bajra grains may be cooked with rice or fried, or they may be ground into a flour and made into unleavened bread or chapatis, or the flour may be cooked into a paste and eaten as a gruel In the areas where bajra is used as food,

Fig 10 7 A bajra plant that escaped damage from attack by stem borers which killed or severely injured surrounding plants of sorghum

it is generally the preferred cereal during cool weather Very little is known about the characteristics of the kernel that determines good quality, but generally a lustrous, bold, pearly amber grain is desired

The fodder of bajra is generally considered to be poor in quality Breeding to improve tillering capacity, leafiness, ability to retain green colour, and juiciness of stems would increase yield and nutritive value of the fodder

RAGI (Finger Millet)

Ragi or finger millet is the most important of the lesser millets in India Ragi is believed to be indigenous to India It is cultivated in India, Ceylon, Malayasia, China, Japan and Africa The largest acreages in India are found in Madras and Mysore states, but it is also grown in Maharashtra, Andhra Pradesh, Uttar Pradesh, and Bihar It is a short duration crop, usually grown under rainfed conditions on the less fertile and droughty soils It may be grown in periods of high temperature It responds to high fertilization and adequate moisture and will produce large yields under favourable conditions Ragi is a food of the poor people, who grind it into flour which is used in making chapatis or unleavened bread

BOTANY

Ragi, *Eleusine coracana* (L) Gaertn , has a chromosome number of $2n=36$ Several other species of *Eleusine* are known in the tropical areas of the old world, of which the most common is *E indica*, which has a chromosome number of $2n=18$ *E coracana is supposed to have been derived from E indica* [5]

The inflorescence of ragi consists of a group of digitately arranged spikes, the fingers, with one spike the thumb, generally below the main terminal group (Fig 10 8) There is considerable variability among varieties in the arrangement of the spikes The spikelets are crowded into two overlapping rows on the outer sides of the spike Each spikelet contains from 4 to 6 flowers The flowers are perfect except for the terminal flower which may be either staminate or sterile The flowers overlap each other forming a compact tapering spikelet Each perfect flower contains three stamens, a branched stigma and two lodicules The carpel is closely covered by the palea

The spikes may take 6 to 8 days to complete flowering [2 3] The top flower opens first with flowering proceeding downwards, but within a spikelet the lowest flower opens first and the process continues upward The flowers open between 1 and 5 A M Pollen viability is very short, lasting only 10 to 15 minutes Flowering takes place simultaneously in all fingers (Fig 10 8A) The anthers require about 45 minutes for dehiscence after emergence Thus delay in opening permits emasculation after the anthers have emerged The stigma remains receptive for about five minutes after emergence from the glumes

Since the period of anthesis is very short, self-pollination is the rule However, a very small percent of natural cross pollination may occur

Several methods have been proposed for emasculation and artificial cross pollination [1 2] With hand emasculation the flower is selected on the evening previous to its natural opening Other

10 8A

Fg 10 8 Ragi A Spike in flower B Mature spike

10 8B

flowers in the spikelet are cut off and the three stamens of the selected flowers are removed after gently separating the lemma and palea. Hand emasculations are difficult to make due to the small size of the flowers and are usually carried out under a magnifying glass The delayed opening of the anther after emergence may be utilized also in making emasculations A wide test tube or small flask lined with moist filter paper is inverted over the flower and plugged with cotton. The anthers emerge intact without shedding and may be cut off and removed[2 7] Hot water may be used in making emasculations Immerse on for 2—2½ minutes at 52 Centigrade is said to give good pollen killing

Pollinations are made by collecting ripe anthers and breaking them over the stigmas or by dusting a flowering branch of the male parent over the emasculated spikes The contact method in which heads of the two varieties are put together under bags may also be used without emasculation If the male parent has a dominant marker gene F_1 plants with dominant characters may be identified. The contact procedure gives a small percentage of crossing but one F_1 plant is generally sufficient since it will produce several thousand seeds

CLONAL PROPAGATION

Ragi may be clonally propagated by separating tillers and replanting in moist soil as was described in the chapter on Breeding Rice This is a useful procedure for increasing seed production from individual plants for maintaining F_1 plants to test against subsequent generations or for increasing seed supply in early stages of increase of a new strain or variety

GENETIC STUDIES

Polyploid origin for *E coracana* is suggested since it has a chromosome number of $2n$ 36 and the basic chromosome number of the genus *Eleusine* is 9 That the species is a polyploid is further indicated by possession of duplicate genes for inheritance of many characters The inheritance of many qualitative characters such as purple pigmentation grain colour sterility per carp colour elongation of earheads glume length and earhead shape have been studied.[7] Very few genetic studies have been made of characters important in breeding

VARIETIES

Varieties of ragi have been developed for various states and climatic areas of India.[4] Students should

consult the Agriculture Department, Extension Service, Agricultural College, or Agricultural University in their area for names of locally adapted varieties

METHODS OF BREEDING

Ragi is a self pollinated crop Breeding methods normally followed in the improvement of self-pollinated crops will be utilized in improvement of ragi These include introduction, selection, and hybridization

Since ragi has been grown in India for a very long time, introduction has not played a very important part in improvement of ragi in recent times. Building up a collection of ragi germ plasm, obtaining both exotic and indigenous collections, is a necessary step to provide future breeding materials Currently about 700 strains are being maintained in India by the Indian Agricultural Research Institute, New Delhi

Both mass and pure line selection have been used in the past to isolate improved strains from mixed local varieties Many of the improved varieties grown in the different states in recent years were developed by pure line selection

Hybridization has been used to develop many of the currently grown varieties These include Cauberg and Purna from Mysore, Co 1, Co 7, and K2 from Madras, Vizianagaram 1 and 2 from Andhra Pradesh, A 404 and A 407 from Bihar, and T-36 from Uttar Pradesh

BREEDING OBJECTIVES

Yield, early maturity, lodging resistance, disease and insect resistance, and quality are all important objectives in breeding

Yield. Higher grain yield is the principal objective in breeding ragi Although the average yields of ragi are generally very low, this is because the crop is usually grown under unfavourable fertility and cultural conditions Ragi has potentially high yielding ability and yields of 5,000 kilos/hectare have been obtained in national demonstration trials in cultivators' fields Ragi has a deep root system and is capable of feeding in the lower soil zones It also has a high photosynthetic area Factors to select for are vigorous growth and high tillering capacity Along with high potential yielding ability, resistance to lodging and diseases will increase the total harvested yield

Maturity. Ragi varieties may be grouped on the basis of maturity into early (80 to 100 days), medium late (100 to 120 days), and late (120 to 145 days) Improvement should normally be directed toward the early and medium late varieties There are several advantages of early maturity In peninsular India it is possible to grow three crops of ragi per year if early varieties and irrigation are available Early maturity adapts ragi to multi-cropping and it may be filled in between an early rabi and a kharif crop if irrigation is available By growing an 80 day variety for 20 days in the nursery bed and transplanting, only 60 days is required in the field Photoperiod insensitive varieties will permit the same variety to be grown in all seasons

The ragi plant has both basal and nodal tillering Basal tillering permits uniform ripening and harvesting High basal tillering tends to result in late maturity, so selection for early maturity and high tillering capacity in the same plant is not always fruitful Nodal tillering results in late maturity and uneven ripening

Lodging Resistance. More lodging resistance is needed as existing commercial varieties tend to lodge under high fertility Co 7 is one of the best in lodging resistance [5] There are dwarf types in the Indian millet collection which might be useful in breeding for lodging resistance

Disease and Insect Resistance. The principal diseases of ragi in India are blast, seedling blights and wilt, downy mildew, and smut Helminthosporium leaf spot and other leaf spots may also occur

A BLAST Blast is caused by a species of *Piricularia* The identity and exact name of the species appear to be still in question [6] The disease may be severe and in some years causes widespread damage in Madras state and other areas of south India Infection may occur as early as the seedling stage with grey-green to yellow lesions forming on the leaf blades Later the main stem becomes infected and the earhead breaks over Grains which form may be shrivelled and light in weight Losses up to 80 percent have been reported depending upon the time of infection Commercial varieties are generally susceptible The ragi collection of 700 types from I A R I has been screened in the field at several locations but the observations have generally been masked by the presence of other diseases

B SEEDLING BLIGHT Seedling blight, caused by *Cochliobolus nodulosus* Luttrell, is widespread in India and other countries and causes heavy losses in years with high continuous rainfall[6] The disease occurs in all stages of growth from seedling to the mature plant and may infect all parts of the plant Varieties now cultivated are mostly susceptible and little is known regarding sources of resistance

C DOWNY MILDEW Downy mildew, incited by *Sclerophthora macrospora*, may cause severe damage to ragi[6 9] Outbreaks have been reported from Mysore and Madras states in India Plants are stunted and leaves may arise close together giving the appearance of being in a bunch No information is available on varietal resistance

D SMUTS Smut, caused by *Melanopsichium eleusinis*, is found on ragi in some areas in India No information is available on sources of resistance to this disease

E INSECTS Stem borers cause damage to the ragi plant but no work on breeding for resistance to insects has been initiated

Quality. Ragi grain is a staple food in Mysore and other areas of south India The proteins of ragi are said to be complete proteins containing most, if not all, of the essential amino acids There is little information available, however, on the quality characteristic desired in ragi Larger seed size, white seed colour and improved nutritive value would all be desirable A white grained ragi variety has been developed in Madras state[10] Open fisted spikes are preferred to the tight ones for growing in rainy seasons as they dry out better and produce brighter seed

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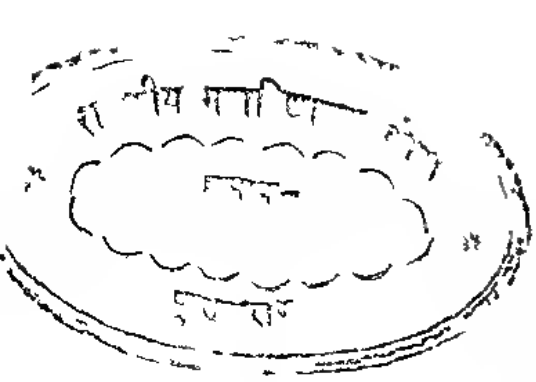


11

Breeding Cotton

Cotton is indigenous to south and southeast Asia and has been cultivated in the Indus valley for more than 5 000 years Relics of the Mohen-jo-daro period indicate a high degree of art in spinning and weaving with cotton at that time India possessed a flourishing export trade in cotton and cotton fabrics in early historic times Cotton was also indigenous to the Americas and was grown and used for clothing in Brazil, Peru, and Mexico long before the discovery of America

India now grows the largest acreage of cotton of any country in the world, over 825,000 hectares, but in total production it falls far below the U S A , and also below Russia which has only about one-fourth the acreage of India [55] About 3 5 million acres of cotton are grown in Pakistan, much of this under irrigation In India cotton is cultivated from the lower Himalayas in the north to the extreme southern tip, but about 90 percent of the acreage is in peninsular or southern India

The acre yield of cotton in India is the lowest of any major cotton growing country In India, cotton is planted mostly at the beginning of the monsoon and is dependent upon the distribution of rainfall throughout the season Unevenness of rainfall combined with low soil fertility, lack of fertilization, use of unproductive varieties and poor cultural practices account for the low production

The breeding problem in India is complicated by the large scale commercial production of three species and limited production of a fourth species within the country Before the introduction of the American long staple, *Gossypium hirsutum* species in the last century, the Indian cultivated cottons were mainly of the desi, short staple, *G aboreum* and *G herbaceum* species A very small acreage of *G barba dense*, an extremely long staple species, is grown in south India

In 1917, an Indian Cotton Committee was appointed to study and encourage the growth and production of long-staple cotton in India. This led to the formation in 1921 of the Indian Central Cotton Committee Among its other functions the Indian Central Cotton Committee assisted in co-ordinating research on cotton improvement and provided financial and technical assistance to research institutes and state experimental stations working on cotton It established the Institute of Plant Industry, Indore, the PIRRCOM research station, Coimbatore, and other experimental stations where breeding and other researches on cotton are conducted, and the Technological Laboratory Bombay, which assists cotton breeders with evaluation of the spinning qualities of new varieties As a result of this research many new and improved cotton varieties have been distributed which are now planted on over 70 per cent of the cotton acreage in India Since 1965, the research of the Indian Central Cotton Committee is being integrated into that of the Indian Council of Agricultural Research

There are many problems with cotton which can be solved best by plant improvement Diseases and insects take large tolls from the potential cotton production, a loss that could be reduced if resistant varieties were available The increasing competition between cotton and synthetic fibres requires that more attention be given to fibre quality and to the breeding of varieties with specific fibre properties These and other problems will continue to challenge the cotton breeder for many years to come

ORIGIN AND SPECIES OF COTTON

Cotton belongs in the genus *Gossypium* Although 20 species were described by Hutchinson, Silo and Stephens in 1947,[25] Saunders[53] now recognizes 23 species of *Gossypium* and these are listed in Table 11 1 They include both wild and cultivated species

Table 11.1. Species of *Gossypium* Grouped by Chromosome Number and Geographic Origin[a]

Species	Chromosome 2n number	Chromosome size	Genome symbol	Geographic origin	Use
			Diploid, Old World species		
G herbaceum	26	large	A_1	Asia	cultivated
G arboreum	26	large	A_2	Asia	cultivated
G anomalum	26	medium	B_1	Africa	wild
G triphyllum	26		B_2	Africa	wild
G sturtii	26	very large	C_1	Australia	wild
G robinsonii	26		C_2	Australia	wild
G australe	26		G_3	Australia	wild
G stocksii	26	large	E_1	Indo Arabia	wild
G somalense	26		E_2	Arabia India	wild
G areysianum	26		E_3	Africa	wild
G incanum	26		E_4	Africa	wild
G longicalyx	26		E_5	Africa	wild
			Diploid, New World species		
G thurberi	26	small	D_1	N America	wild
G armourianum	26	small	D_2	N America	wild
G harknessii	26	small	D_3	N America	wild
G klotzschianum	26	small	D_4	Galapagos and N America	wild
G aridum	26	small	D_5	N America	wild
G raimondii	26	small	D_6	S America	wild
G gossypioides	26	small	D_7	America	wild
G lobatum	26			America	wild
			Tetraploid, New World species		
G hirsutum	52	26 large, 26 small	$(AD)_1$	N America	cultivated
G barbadense	52	26 large, 26 small	$(AD)_2$	S America	cultivated
G tomentosum	52	26 large, 26 small	$(AD)_3$	Hawaii	wild

[a] Adapted from Hutchinson,[25] Saunders,[41] and Stephens[49]

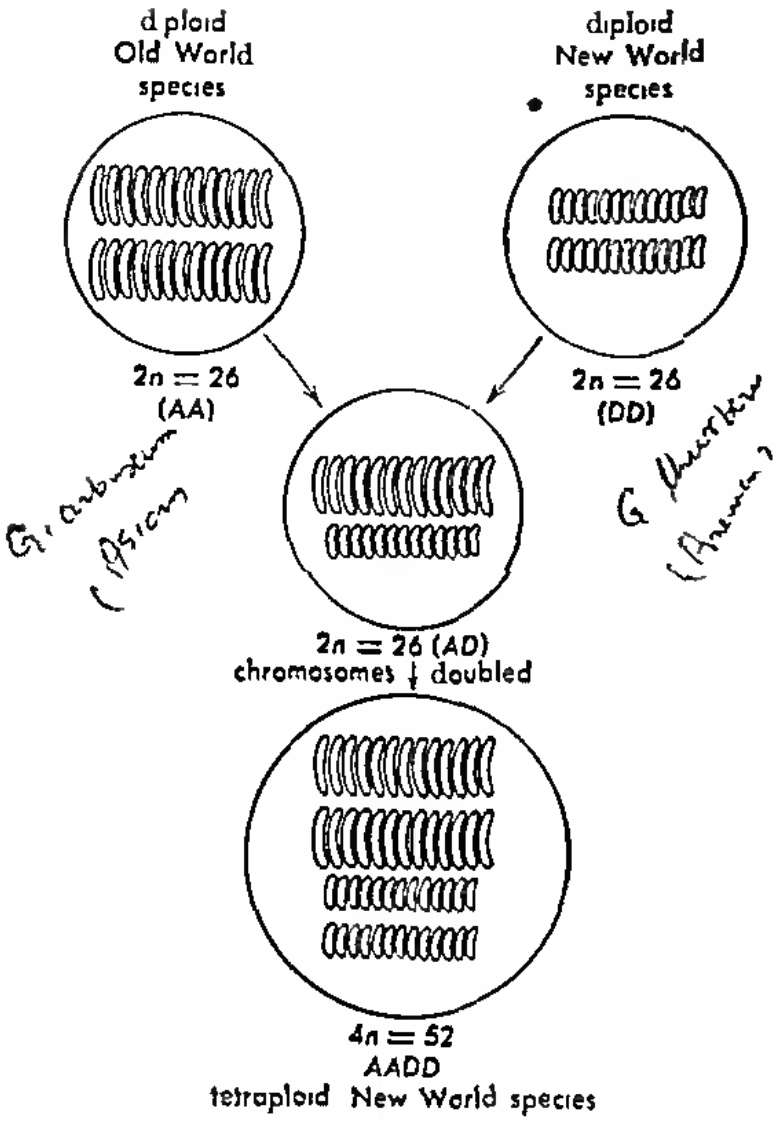


Fig 11 1 Origin of tetraploid cotton The origin of tetraploid, New World species of cotton has been demonstrated by crossing an Asiatic cultivated (diploid) species with an American wild (diploid) species and doubling the chromosomes of the hybrid plant The amphidiploid produced was cross-fertile with American tetraploid species

and Old and New-World species The species of Hutchinson *et al* are also described in the ICAR Monograph, *Cotton in India*, by Gadkari[16] and by Sikka and Joshi [57] Numerous races of many of these species are also recognized The cultivated species have spinnable seed fibres called lint. The wild species have only short seed fuzz or smooth seeds Many of the wild species are perennial shrubs

In Table 11 1, the species of *Gossypium* are grouped according to chromosome number and geographic origin Twelve of the species, all of which have the chromosome number $2n=26$, are indigenous to the Old World (Asia, Africa, or Australia) Eight species indigenous to the New World also have the chromosome number $2n=26$, but the chromosomes in the New-World species are comparatively smaller in size than the chromosomes in the Old World species Three tetraploid species, with the chromosome number $2n=52$, are also indigenous to the New World Each of the tetraploid species has 26 large and 26 small chromosomes This suggests that the tetraploid New World species may be allopolyploids which originated by hybridization between Old World and New-World diploid species (Fig 11 1) [65] This probable origin was demonstrated experimentally by crossing *G arboreum* (Asiatic cultivated, $2n=26$) $\times$ *G thurberi* (American wild, $2n=26$) and doubling the chromosomes of the sterile hybrid with colchicine [7 19] The resulting amphidiploid ($2n=52$) crossed and produced partially fertile hybrids with the New World tetraploid cottons There is a high degree of chromosome homology between species with the same chromosome number and from the same geographic area. Homology is not complete indicating differentiation of the chromosome complement to some extent

The original cultivated Asiatic cottons belong to the species *G arboreum* and *G herbaceum*, both of which have short staple length (Fig 11 2) [55] *G arboreum* is the principal form presently cultivated in India comprising about 40 percent of the total cotton acreage *G arboreum* is cultivated in almost every cotton growing state in India but largest acreages are found in Rajasthan, Madhya Pradesh, Maharashtra, Andhra Pradesh and Madras states. *G herbaceum* is grown on about 30 percent of the total cotton acreage in India, principally in Gujarat, Mysore and Andhra Pardesh *G hirsutum* is also grown on about 30 percent of the total cotton acreage in India and is the principal type in Punjab and Madras, but it is also grown in Rajasthan, Madhya Pradesh, Maharashtra, and Mysore states. The latter species is best adapted to areas with irrigation or where rainfall is assured In areas where rainfall is uncertain and irregular, so that the crop may be damaged either by drought or by excessive rainfall, the hardy, Old World species are best adapted. The long staple *G hirsutum*, or American upland as it is generally known, was first introduced into Bombay from America in 1790 but introductions were continued throughout the 19th and the early part of the 20th century with varying degrees of success Most of the early intro-

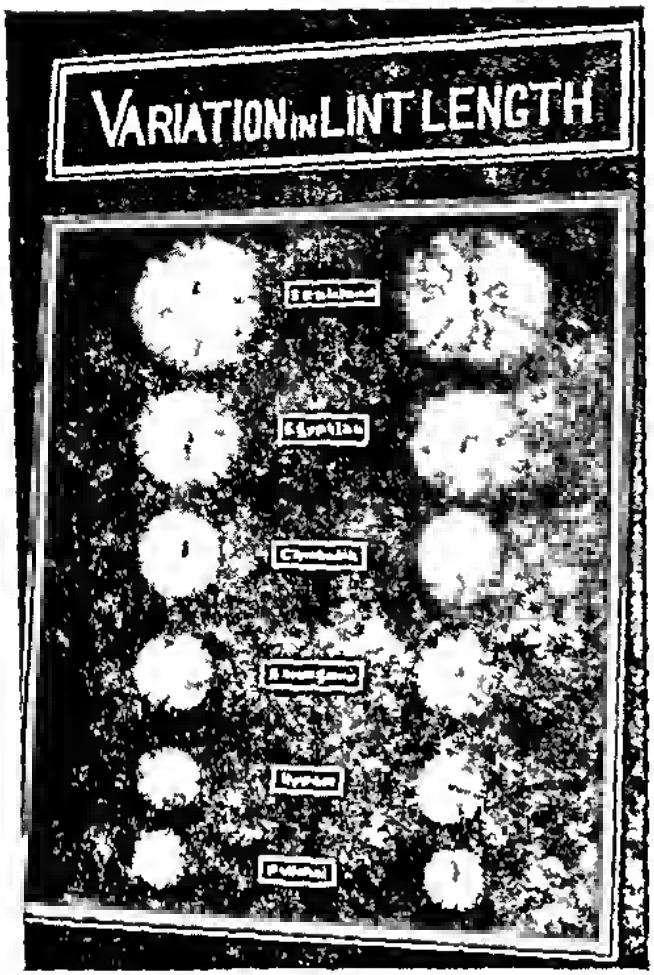


Fig 11 2 An exhibit showing variation in lint length of some cottons They are (from top to bottom) Sea Island (*G barbadense*) Egyptian (*G barbadense*) Cambodia (*G hirsutum*) Karunganni (*G arboreum*), Uppam (*G arboreum*), Pul chai (*G herbaceum*)

ductions failed owing to attacks of jassids or leaf hoppers However, some upland type plants with more leaf hairs persisted in fields of desi cottons and these formed the basis for selections in later years that successfully established the Punjab American upland cotton as a crop in India and Pakistan [23] Another strain of upland cotton in India came from Cambodia Cambodia cotton, too had dense leaf hairs Cambodia cotton was carried by the Spaniards from Central America to the Philippines, from there it got to India via Cambodia *G hirsutum* originated in southern Mexico and Central America as a perennial shrub, through breeding it has become an annual *G barbadense* has been introduced into India, for the most part without success, however, recently a small acreage is being grown in the coastal areas of Mysore, Madras and Kerala Nearly ninety percent of the cotton area in Pakistan is planted to *G hirsutum* and the rest to *G arboreum* [1]

VARIETIES OF COTTON

The cultivated varieties of cotton grown in India are comprised of complex groups of materials adapted to local conditions in the various cotton growing regions During recent years many new agricultural varieties have been developed Many of the new varieties originated from crosses involving older varieties, races, or species

Trade Varieties of Cotton. The cottons grown in different regions of India are known by various trade or commercial names These trade names originated primarily in relation to a port or area through which the cotton was marketed However, these names became so well established that the various cottons are still referred to by these names both in common use and in literature A trade variety may include different races, species or even their mixtures The principal trade varieties are listed below according to the regions of their cultivation [11 56]

1 Northern *hirsutum arboreum* Region This region includes Punjab, Rajasthan and Uttar Pradesh The varieties grown in this region are called Bengals and Punjab American The Bengals include the *arboreum* varieties of the race *bengalense* and the Punjab Americans include the *hirsutum* varieties

2 Southern *hirsutum arboreum herbaceum* Region This region centering in Madras state grows all three species of cotton The *arboreum* varieties of this region are mainly of the *indicum* race The trade varieties of this region are Karungannies, Nadam, Uppam, Bourbon and Cambodia The trade name Tinnies is also used for Uppam, Nadam and Bourbon Another trade name, Salem, is used for the latter two types Bourbon and Cambodia cotton are varieties of *hirsutum* Although originally of American origin, the Cambodia stock was introduced into India as a bulk from Cambodia in 1906

3 Western *herbaceum* Region This is the *herbaceum* cotton area in Gujarat state The trade varieties of this region are Surti Broach and Wagad

4 Central *arboreum* Region This is the *arboreum* tract in Gujarat, Maharashtra and Madhya Pradesh states The trade name for varieties of this region is Oomras The Oomras varieties are

of *bengalense* race of the *arboreum* species, mixed or unmixed with *hirsutum*

5 Central *hirsutum arboreum herbaceum* Region This region includes Mysore, Andhra Pradesh and Orissa The trade varieties of this region are Oomras, Hyderabad Gaorani, Mungari, Cocanadas, Chinnapathi and Northerns of *arboreum* species, Kumpta, Westerns, and Uppam of *Herbaceum* species, and Cambodia of *hirsutum* species All of these trade varieties are jointly called Southerns

6 Eastern Region The eastern region consists of Assam, Manipur and Tripura and grows *arboreum* varieties of the *cernum* race The cottons of this region are called Comilla cotton Sometimes they are also referred to as Garo Hill cottons

The above division of the country into regions is extremely complicated Presently, there is a tendency to divide the cotton growing areas of the country into four regions only, viz northern, central, southern and eastern regions Recent varieties grown in these regions are listed in Table 11 2 Since recommended varieties change frequently, as improved strains are developed, the student will need to consult the Agricultural Department, Agricultural College or Agricultural University in his area for current lists of recommended varieties

POLLINATION IN COTTON AND VARIETAL PURITY

The base of the cotton flower is surrounded by three leaf like triangular bracts forming what is commonly known as squares (Fig 11 3) On the day preceding pollination the twisted corolla emerges from the bracts When the corolla first opens the petals may be white, cream, yellow or purple in the different varieties (Fig 2 2) The following day the corolla turns pink, gradually changes to red, and finally falls from the plant (Fig 11 4) The stamens are numerous, forming a tubelike staminal column around the style which is united with the inside base of the corolla The pistil is formed from three to five carpels corresponding to the number of locks in the boll Pollen is shed directly on the stigma when the anthers open, or it may be carried to the stigma by insects Pollen is wind-borne only to a very slight extent, if at all, on account of its heavy sticky nature, but pollen carried by insects may result in considerable cross pollina-

Table 11.2. Species and Varieties of Cotton in India According to Geographical Region.[a]

Cotton growing region	*States included*	*Species of* **Gossypium**	*Recent varieties*[b]
Northern region	Punjab Rajasthan Uttar Pradesh	*hirsutum* *arboreum*	216F, Indore 1 Ganganagar, 320F, LL54, H 14 231R, Ranibeni
Central region	Gujarat Maharashtra Madhya Pradesh	*herbaceum* *hirsutum* *arboreum*	Kalyan, Digvijay, Deviraj, 134-Co, 2-M, C J 73, Virnar, Buri 147, Gaorani 22, G 46, Daulat
Southern region	Madras Andhra Pradesh Mysore	*hirsutum* *arboreum* *herbaceum* *barbadense*	MCU 2, MCU 3, 216F, Parbhani-American, K 6, K 7, Jayadhar, Laxmi, Sel 69, Westerns 1, Cocanadas 2, N 14, Nandium, Adonicum, Andrews
Eastern region	Assam Tripura Manipur	*arboreum*	D 46 2-1

[a] Adapted from Sikka and Joshi [56]

[b] Recent varieties may be pure *hirsutum arboreum* or *herbaceum* types or may be mixture of types because of interracial or interspecific crosses involved in the varieties

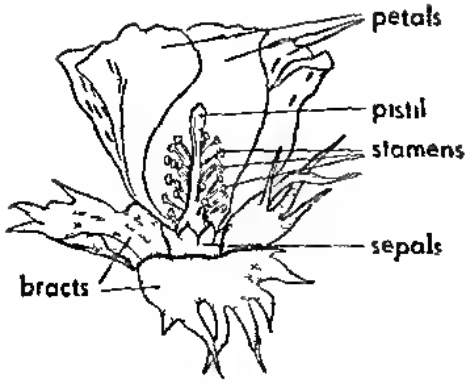


Fig 11 3 Cotton flower with petals cut away

tion [71] The amount of cross pollination normally ranges from 5 to 25 percent although amounts in excess of 50 percent have been reported [2 62 70] The amount of cross-pollination depends more upon the relative abundance of pollen carrying insects than any other factor Most natural crossing occurs between plants growing only a few yards apart, however, cross pollination has been reported at distances up to several hundred metres [9] Different amounts of cross pollination have been observed also with different varieties [64]

Fig 11 4 Cotton flower closed after pollination The petals turn pink or red the day after pollination and later fall from the plant

A simple technique has been developed for artificially cross pollinating cotton flowers [15 71] Crosses are made on the day preceding that in which the flowers would open normally (Fig 11 5A) The corolla is cut away with small scissors or a curved scalpel and the anthers are removed (Fig 11 5B and C) Pollen is collected from the male flower in a short length of a soda straw (Fig 11 5D) The soda straw partly filled with anthers is slipped down over the exposed stigma (Fig 11 5E) The bracts are pulled up around the soda straw and wired securely to hold the soda straw in place (Fig 11 5F) Some breeders recommend emasculating one day and pollinating the next, but this procedure may result in unnecessary drying out of the stigma About 75 percent of normal seed set may be obtained after artificial crossing

When cotton plants are to be selfed, it is necessary for the flower to be covered to prevent cross pollination A small paper bag is placed over the bud the afternoon before it opens (Fig 11 6A) If placed over the flower too far in advance of opening the temperature within the bag may become so high as to cause shedding of the boll Foreign pollen may also be excluded from the flower by fastening the tips of the corolla together with paper clips, rubber bands, collodion, or a small tag strung with fine wire or string (Fig 11 6B) F ization is completed in 36 to 40 hours after pollination

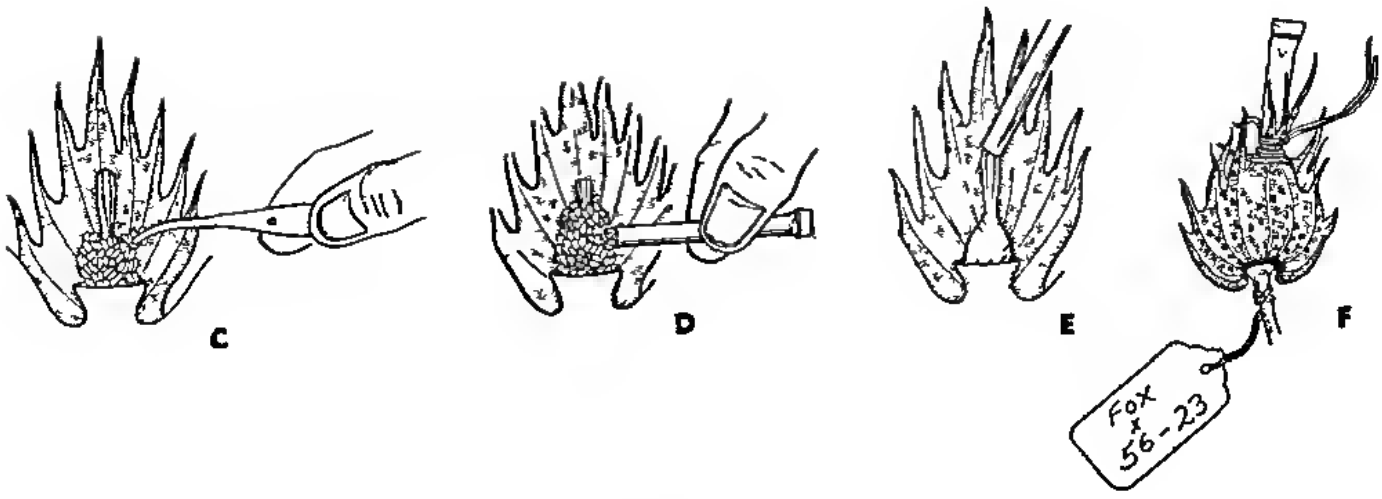
Cross pollination in cotton leads to an increase in heterozygosity in the cotton plant This results from crosses between (*a*) genotypes within the variety (varieties are never pure lines as in self pollinated cereals), (*b*) varieties and mechanic mixtures of other varieties within the same [illegible] and (*c*) varieties in adjacent fields. Hybrid plan resulting from cross pollinations in turn cross with other plants within the variety, and thereby add the genetic mixture It has been demonstrated that a moderate degree of heterosis accompanies he zygosity in an open pollinated variety and is desirable in order to maintain maximum yield adaptation [60]

There is some controversy about how much crossing and mixing may affect the deterioratio of varietal purity The apparent "running out"

11 5A

11 5B

Fig 11 5 Steps in crossing cotton A Cotton flower at suitable stage for emasculation and crossing B Cotton flower with sepals and petals cut away preparatory to emasculation. At this stage the anthers are compressed around the staminal column with the stigma protruding from the tip C Removing the stamens with fine pointed tweezers D Collecting ripe anthers from a flower on the pollen parent with a short section of a soda straw The end of the straw is crimped to hold the anthers E Slipping the soda straw containing the ripe anthers over the stigma of an emasculated flower F Bracts wired around the soda straw holding it in place over the style, thus protecting the stigma from foreign pollen The wire also holds a tag on which the cross is recorded



11 5C—F

Fig 11 6 Methods of preventing cross pollination in cotton A Flower covered with paper bag B Corolla tip fastened with a fine wire or string

cotton varieties necessitates cultivators buying new seed at regular intervals to keep an improved variety pure When large numbers of varieties are grown in a community natural crossing between varieties and varietal mixtures is inevitable As a result varieties deteriorate in purity very rapidly There is evidence that varieties which are more uniform in plant type and other characteristics deteriorate less rapidly In areas where many varieties are grown and cross pollination is high owing to large insect populations seed could become mixed in one season to a greater extent than in several seasons in an area where only one variety is grown

GENETIC STUDIES

Extensive genetic studies of cotton have been carried out and several comprehensive reviews of the literature have been made [18 58 68 69] Over 150 genes have been identified [58] mostly for simple morphological characters but this list also includes many genes for disease resistance hairiness, and other useful agronomic characters The inheritance of several of these will be discussed later in the chapter with the objectives of breeding for specific characters

Many cytological studies have been made in regard to speciation of *Gossypium* Some of these have already been referred to in the discussion on the origin of the diploid and tetraploid species [6 7 19 57 58 69] These studies have contributed to an understanding of the genetical relationships between the wild and the cultivated cottons and have provided the basic knowledge required for the transfer of many useful genes from the wild species to the cultivated cottons [23]

The identification of genes for specific characters has been aided in recent years by the development of *monosomics* for several chromosomes in the amphidiploid species *G hirsutum* [10] By the utilization of monosomics (chromosome number of $2n$ 1) it is possible to determine the contribution of individual chromosomes a technique used successfully for the identification of genes in the hexaploid and tetraploid species of wheat

Haploid plants are sometimes found in cotton and these may be used for the production of *doubled haploids* Haploids may be identified by a thin stem short internodes small leaves and floral parts and failure to shed pollen [41] They usually lack seed and bolls and may be taller than the normal plants in the field Haploids occur usually as twin seedlings once in about every 50 000 to 100 000 plants in upland cotton [68] Chromosome number of haploids may be doubled by repeated application of 0 2 percent colchicine solution to the meristems of grafted plants until doubled sectors appear [41] Doubled haploids hold considerable interest for cotton geneticists since they are extremely uniform Doubled haploids are comparable to pure lines in self pollinated crops or inbred lines in maize and can be maintained by controlled self pollination Unlike maize inbreds doubled haploids are usually vigorous *If* a procedure for producing hybrid cotton commercially becomes available doubled haploids might prove useful as parent lines

Several male sterile genes have been identified in cotton to which have been given the symbols ms_1 ms_2 and so on The ms_1 and ms_3 genes are recessive but confer only partial male sterility The ms_2 gene also is recessive but gives complete male sterility One gene, Ms_4, is dominant for male sterility Extensive tests have been made with the ms_2 gene to check for cytoplasmic genetic inter

actions but so far no cytoplasmic influence in relation to the gene has been established [38] Cytoplasmic male sterility has been obtained in cotton plants with *G anomalum* cytoplasm [42 43] The cytoplasmic male sterility resulted when an amphidiploid of the cross *G anomalum* × *G thurberi* was backcrossed with *G hirsutum* as the pollen parent Reciprocal crosses with *G hirsutum* cytoplasm gave fully fertile plants The sterility was expressed as a reduction in the number of fertile anthers Sterile plants contained a partially recessive gene in the homozygous condition

METHODS OF BREEDING COTTON

The methods of breeding new varieties of cotton are not as clear cut and well defined as methods of breeding self pollinated crops like wheat or rice, or even methods of breeding a cross pollinated crop like maize In fact many breeders have a particular system which they practice, both for constituting a new variety and for improving it from time to time The differences in their breeding systems are generally differences in detail of how lines or families are combined rather than in the over-all procedures of selection or hybridization

In self pollinated crops individual plants are highly homozygous By starting with individual plant selections, pure line varieties are developed which remain uniform in appearance until mechanical mixture with other varieties, natural hybridization, or mutations render them impure In a naturally cross pollinated crop like maize, each plant is highly heterozygous By continuous selection within selfed lines, true breeding inbred lines of maize may be developed, but the purification is accompanied with a marked decrease in vigour Cotton plants are neither as homozygous as the self pollinated cereals nor as heterozygous as open-pollinated maize Although most flowers on the cotton plant are generally self pollinated, cross pollination is always sufficient to maintain many heterozygous alleles The amount of the cross pollination varies from field to field, depending to a very large extent upon the insect populations present The lack of uniform breeding methods within the cotton crop stems largely from differences in the genetic condition within the cotton plant

The methods employed in breeding new varieties of cotton may be grouped broadly into introduction, selection, and hybridization as with self pollinated crops, but different procedures in carrying out these methods are practiced

Introduction and Acclimatization. Improvement of cotton in India was started as far back as 1790 At that time large quantities of Indian cotton were exported to England, yet England had to depend on America for the best quality cotton In their eagerness to capture a part of this market, the East India Company started extensive trials in India toward the end of the eighteenth century with introduced varieties mainly of *hirsutum* origin Over the next 100 years many introductions were made of American, Brazilian, Peruvian, Egyptian, Sea Island, and other foreign cotton varieties [55] These introductions met with varying degrees of success, but for the most part they were outright failures

Introductions may be grown as introduced, *en masse* they may be improved by natural or artificial selection, or they may be used as parents in a hybridization programme Most of the failures of the cottons introduced into India were apparently due to trying to grow *en masse* introduced varieties on a commercial basis in areas where they were not adapted In this connection it must be remembered that those responsible for the early introductions did not have available the scientific knowledge that we have today Currently we would introduce and assemble large collections of varieties of types known to be genetically different, grow them in the various agroclimatic areas, and then select those strains which appear to be adapted for further testing and study Only after it is proven to be productive in a particular area would a variety be sent to the cultivator for production In a few areas of India variety types did emerge from the early introductions which are now grown successfully Examples are the Punjab American cottons currently grown in Punjab and Pakistan and the Cambodian cotton of south India [1,45] For success to be attained by selection, either natural or planned, there must be genetic variability in the introduced variety The partial cross pollination in cotton provides for this genetic variability and permits a certain amount of natural selection or acclimatization to occur

To a large extent the lack of adaptation of the early introductions of *G hirsutum* varieties into India was due to their susceptibility to jassid attacks or unfavourable photoperiodic response [23]

The cottons from Central America are short day types and do not respond favourably to long days Cambodia cotton of south India, originally from Central America, has never been successful in the longer days of north India or Pakistan Cambodia cotton had long dense leaf hairs and was therefore able to survive the jassid attacks It was a hardy and vigorous strain and yielded well, so its cultivation spread rapidly in south India after its original introduction in 1906 The American Upland varieties from the U S Cotton Belt had been selected there for fruiting under longer days and when introduced into northern India or Pakistan were unaffected by the day length there They were severely injured by jassids, and quickly went out of cultivation Occasional upland plants with greater leaf hairiness were able to persist, however, in fields of Old World cotton From these mixed crops the present American Upland types of Punjab and Pakistan were later selected [23] Such acclimatization would not have been possible in a highly self fertilized crop which lacks the genetic plasticity of the cotton plant

In addition to the *hirsutums* introduced from America, strains have been introduced from Africa A *hirsutum* type from Uganda has been used to improve the staple length of the Cambodia cottons in Madras state Recent introductions into India include a short fruiting branch type of *G hirsutum* from Russia which is being used in breeding experiments in Madras state [61] Andrews, a variety of sea island, *G barbadense*, has been introduced into Madras state

Selection. Selection is practiced both to maintain the purity of existing varieties of cotton and for the development of new varieties A clear distinction cannot always be made between the selection practiced for these two purposes With the variable genetic condition in cotton, as a result of its partial cross pollination, selection is required to maintain varietal purity Often selection directed primarily toward maintaining varietal purity leads to the isolation of improved strains of a variety, or even to a new variety Plants with superior genotypes may originate by selection within hybrid populations Three selection procedures are outlined here, but many modifications of these methods are used by different breeders

A SINGLE PLANT SELECTION Most of the early work on cotton improvement, in India and other countries of southeast Asia, were based on single plant selections The Parbhani-American 1 was selected in Bombay in the year 1932 as a result of single plant selection from a cultivator's field The varieties, Cambodia 1 and Cambodia 2, were selected in Madras in a similar way from Cambodia cotton [45] However, in nearly every case where single plant selection is used to isolate a variety, additional selections are made within the family of the original plant before the variety is finally distributed

Single plant selections from open pollinated cotton will be more or less heterozygous Lines derived from single plants will not be pure (single genotypes) unless the pollination has been controlled to ensure selfing in previous generations Pure-breeding lines may be developed and maintained by selfing and selecting within the inbred progenies Pollination will need to be controlled at each generation to ensure selfing (Fig 11 6) Experimental results indicate that there is usually a reduction of 10 to 15 percent in yield of seed cotton after several years of inbreeding [8 63] The high yield level in many commercial varieties results from the partially heterozygous nature of the lines that go into the variety Equally high yields may not be possible with more homozygous material

B MASS SELECTION A mass selection is developed by bulking seed from open pollinated, or selfed, plants selected on the basis of appearance (phenotype) Progeny testing is not practiced This method of breeding is comparable to the mass selection method of breeding open pollinated maize The individual plant selections are usually made within a variety or a breeding line, and conform, insofar as the breeder can determine by visual inspection, to a desired plant type Rigorous selection for a desired plant type must be practiced over a period of years to obtain uniformity in varieties originating by mass selection This is necessary because the selected plants will be partially heterozygous, and segregation and natural hybridization will occur in succeeding generations Also, plants may appear to be superior due to favourable environment rather than genetic variation In Punjab mass selection was used for purification, improvement, and maintenance of the upland cotton variety 289 F/K 25 [39] The mass selection was effective in increasing gin turn out and staple length, but not yield Mass selection is seldom

used now for the development of new varieties, but is sometimes used to maintain a strain or varietal type

C PROGENY SELECTION In this method of breeding cotton, individual plants conforming to a desirable variety type are selected from pure stocks of the variety Open pollinated or selfed, seed from each plant is planted in a progeny row the following season A group of plant to row progenies that are uniform and meet the requirements prescribed by the breeder for the type of cotton that he desires may be bulked Progenies that are not uniform are discarded or reselected The progeny method is superior to the massing of individual plants because it is based on the performance of selected plants rather than on their appearance alone The progeny test helps to identify plants superior owing to genetic variation from those superior owing to being grown in a favourable environment Progeny selection differs from pure line selection in self fertilized crops in that considerable genetic variability still exists in the progenies that are bulked Owing to the genetic variability, selection must be practiced over and over again Considerable uniformity may be attained for characteristics such as plant type, maturity or fibre properties, which the breeder is using as the basis of selection The plant-to row progeny method of breeding cotton was used before 1900 in the breeding of wilt resistant cottons [67] It is still widely used as a procedure for breeding new varieties and for the maintenance of existing ones

Various modifications in procedure for testing and bulking progenies are practiced by different breeders For example

1 Progeny rows may be replicated and grown in yield tests [24]

2 Selected progeny rows may be bulked to start a new selection cycle and bring the principle of *recurrent selection* into practice This type of selection has been referred to as *mass pedigree* selection [20]

3 A broad selection base may be maintained by bulking groups of progenies, rather than restricting the progenies to be bulked to a narrow range of similar genotypes This principle is referred to as *type selection* [13] Its purpose is to prevent deterioration in yield that might result by restricting the progenies to be bulked to a narrow genetic base

4 *Selection within selfed lines* may be used for the maintenance of varieties Selfed seed from selected plants is grown in progeny rows (Fig 11 7) Selection for next year's progeny row planting is made within these selfed lines Entire progenies may be bulked for seed increase, or selected plants from the progeny rows may be selfed and bulked for seed increase (Fig 11 7) This selfed line selection procedure maintains a high degree of uniformity within the variety and is widely used by breeders in the U S A It is objected to by some breeders as restricting genetic variability and thus possibly leading to reduced yield

5 *Simultaneous maintenance and improvement of existing varieties* may be practiced Phenotypically similar but genetically improved progenies may be entered into the variety complex ! The improved progenies may have been derived by selection from selfed plants, outcrosses or recurrent selection, by hybridization or even by backcrossing By this procedure the performance of a variety may be gradually improved while keeping the general morphological features and adaptation !

Hybridization. Many varieties of cotton have originated from natural hybridization [72] Other varieties have originated by artificial hybridization Examples of varieties developed by hybridization in India are Virnar, H 420, Digvijay, Co 4, and others Co 4 originated from a cross of Co 2, selected from the original *hirsutum* Cambodia bulk introduced in 1906, and A 12, a *hirsutum* type from Uganda, Africa A reselection from Co 4, MCU 1, was crossed with a *barbadense* variety to produce MCU 2 Through this succession of crosses, staple length was increased from less than one inch to about 1 1/8 inches Earlier, hybridization was used less in breeding cotton than with self pollinated crops In cotton considerable heterogeneity exists on account of natural hybridization and segregation It is always possible that superior natural hybrids may be selected and used to establish a new variety But such selection is merely the result of chance, there is need for controlled hybridization in which parent varieties are carefully selected Various types of controlled hybridization have been used, or suggested, for the improvement of cotton

A INTERVARIETAL HYBRIDIZATION Crosses between varieties or strains have been used to develop many varieties, including Virnar, H 420, and Co 4 in India This method of hybridization by which desirable characteristics from the parent strains may

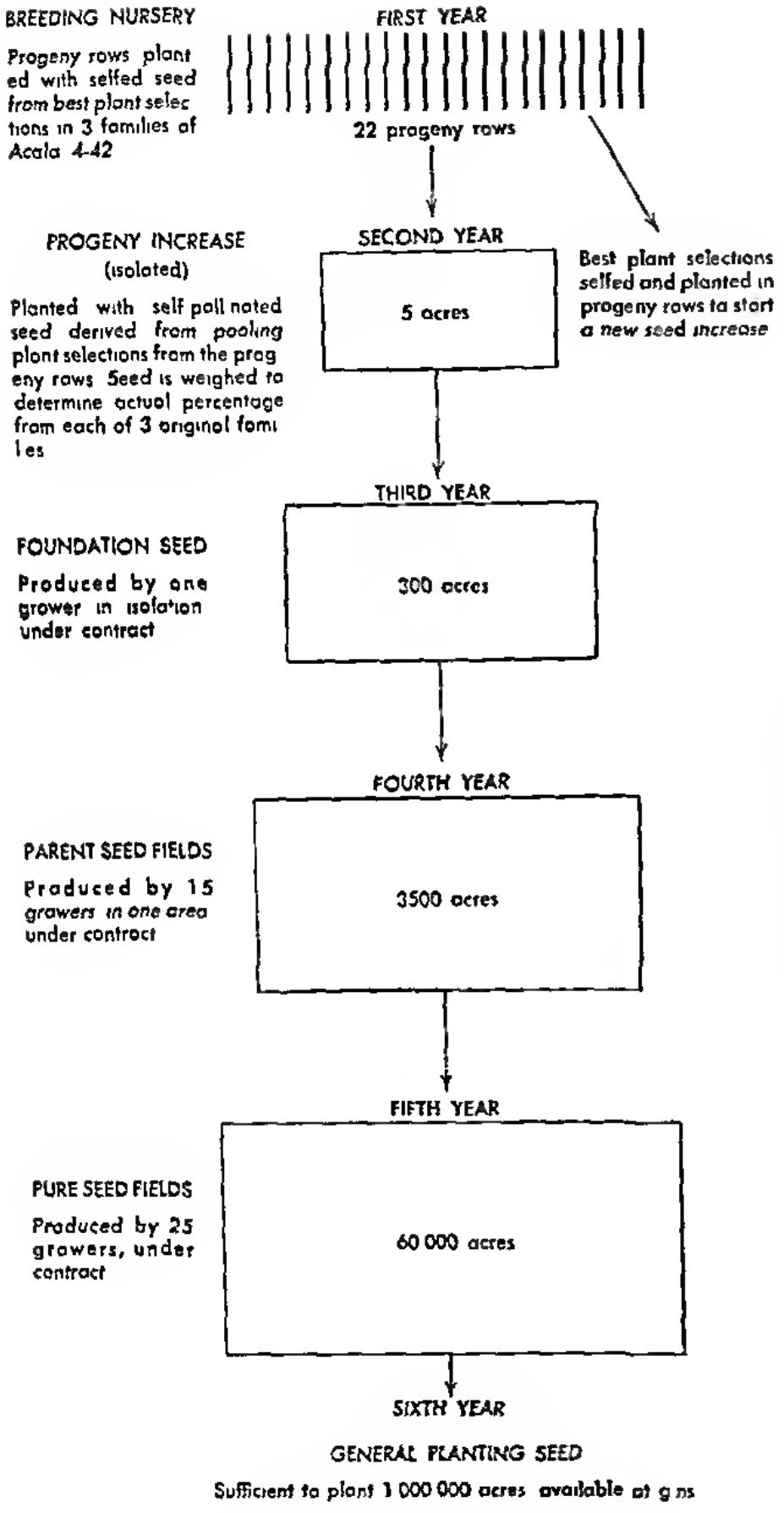


Fig 11 7 Scheme used in California U S A for seed production of the 4 42 variety of cotton A system of selection within selfed lines is used for the maintenance of seed stocks of this variety By modification of this procedure the performance of a variety may be gradually improved while keeping the general morphological features and adaptation

be combined into a single strain or by which transgressive segregations for quantitative characters such as yield or fibre quality might be obtained, has been discussed for the self pollinated crops The use of hybridization in the improvement of cotton does not differ in principle from its use in self pollinated crops, but usually some system of progeny selection will be employed Careful selection of parent material is important for the realization of success in a hybridization breeding programme with cotton as with other crops, in order that desirable characteristics will be combined in the progenies Selection of parents which are not closely related helps in the creation of a broader genetic base as a source of variability In India and Pakistan many races of the indigenous species, *G arboreum* and *G herbaceum*, have been described Crosses among the different races broadens the genetic base, but these wide crosses may bring in problems of sterility

B INTERSPECIFIC HYBRIDIZATION Interspecific crosses may be used to combine desirable genes from two or more species In cotton the crossing problem is complicated by the presence of both diploid and tetraploid species of *Gossypium* (Table 11 1) At the diploid level, the indigenous species, *G arboreum* and *G herbaceum*, are cultivated on a large scale in India The *arboreum* cotton in general have better quality than the *herbaceum* varieties, but the latter are more drought resistant Earlier it was a practice in Madras state to grow mixtures of *arboreum* and *herbaceum* Crosses between the two species have not generally yielded productive types Both species have short staples, below 7/8 inch The diploid species, *G anomalum*, has been used in crosses in India with *G arboreum* to improve fibre fineness and strength [50] Other diploid species which may contribute useful genes to *G arboreum* and *G herbaceum* are *G raimondii*, *G armourianum*, *G somalense*, and others Many interspecific crosses at the diploid level do not produce fertile progenies and this barrier must be overcome before full utilization of genes from other species is attained

Interspecific crosses at the tetraploid level may be made between *G hirsutum* and *G barbadense* In Madras state the variety MCU 2 was developed by crossing a *hirsutum* variety, MCU 1, with the long staple *G barbadense* MCU 2 has longer staple length than MCU 1 The tetraploid species, *G tomentosum*, is reported to be resistant to drought and jassids

Some success has been attained with crosses between the diploid and tetraploids The varieties 170 Co 2 (*G hirsutum* × *G arboreum*) and 134 Co 2M (*G hirsutum* × *G herbaceum*) have been released in Gujarat state [50 56] In the U S A a selection has been obtained from a tri species hybrid (*G arboreum* × *G thurberi*) × *G hirsutum* that has exceptionally strong fibres [32] This is of unusual interest because the factors for fibre strength appear to have been derived from the wild American species *G thurberi* a species which does not produce lint With wide interspecific hybrids several backcrosses to the adapted parent will usually be necessary to recover desirable agronomic characters and to eliminate lethals, sterility, or abnormal chromosome behaviour

C BACKCROSSING The Griffin variety of cotton was developed in 1867 by John Griffin, Greenville Mississippi, by crossing an old upland variety known as Georgia Green Seed with a Sea Island variety, and backcrossing to the upland variety for four or five years [72] This is apparently the first record of the backcross being used for the production of a new variety of any crop The varieties Vijay Kalyan and Digvijay have been developed in India by the backcross in the years 1943, 1947, and 1956, respectively [56] The backcross has been used successfully to transfer disease resistance genes and genes for hairiness to commercial varieties in other countries For example, nine distinct genes for black arm resistance were transferred from four different species of cotton to two commercial strains of Egyptian cotton, *G barbadense* [34 37] Several backcrosses to recover good agronomic characters are generally necessary with interspecific hybrids

D UTILIZATION OF HYBRID VIGOUR The utilization of hybrid vigour in cotton by growing first generation hybrids has been suggested by many workers [33 40 65] As early as 1909 it was suggested that hybrid seed be produced by planting two types of cotton close together and letting insects cross pollinate them [12] Heterosis has been observed in the F_1 of interspecific crosses of cotton for such characters as boll size, number of bolls, length of lint, and general vegetative vigour Heterosis has also been observed in F_1 plants of varietal crosses within the same species [65] To utilize heterosis by growing F_1 hybrids we need, (*a*) a usable form of cytoplasmic male sterility and fertility restoring genes, or other systems for controlling pollination,

(*b*) adequate cross pollination by insects to produce the hybrid seed, and (*c*) means for identifying parents with high combining ability Currently, usable systems of cytoplasmic sterility with pollen restoring genes, such as are used in maize, sorghum, or bajra are not available Chemical gametacides to induce sterility have been tried but are not successful

Suggestions for partial utilization of hybrid vigour by natural cross pollination without emasculation have also been proposed [61] Some of the procedures that might be used include (*a*) planting mixtures of lines with good combining ability in the seed field, (*b*) bulking lines developed by selection without controlled crossing, (*c*) bulking lines after two or three generations of controlled selfing The use of natural cross-pollination would be limited to areas where high insect populations are present so that a high percentage of crossing would be obtained The extent of natural crossing in India and elsewhere is reported to be too limited and the yield increases too low for the success of this method It may be possible to increase the amount of natural crossing by selection Selection for larger stigmas has been suggested as one means of approaching this problem

Irradiation Breeding. Work on irradiation breeding in cotton is very limited Some natural as well as artificially induced mutations have been reported [28 29 58] A variety Indore 2 was developed from x-rayed material of Malwa Upland 4 in Madhya Pradesh and released for cultivation in 1950 [57] A cotton plant with 40 to 50 percent increased hair density has been obtained after x-radiation in the variety Mescilla Acala [29] The increased hair density renders the plant resistant to jassids

Use of Polyploidy. Polyploidy has been used to facilitate interspecific crossing between tetraploid American cottons (n=26) and the diploid Asiatic cottons (n=13) *G anomalum*, a new world wild cotton (n=13) crosses with *G arboreum* as Asiatic cotton (n=13) but the hybrid is sterile When the chromosome number of this hybrid is doubled, the tetraploid thus produced will cross with *G hirsutum* (n=26) [56] Autotetraploids of cotton are usually sterile

OBJECTIVES OF BREEDING COTTON

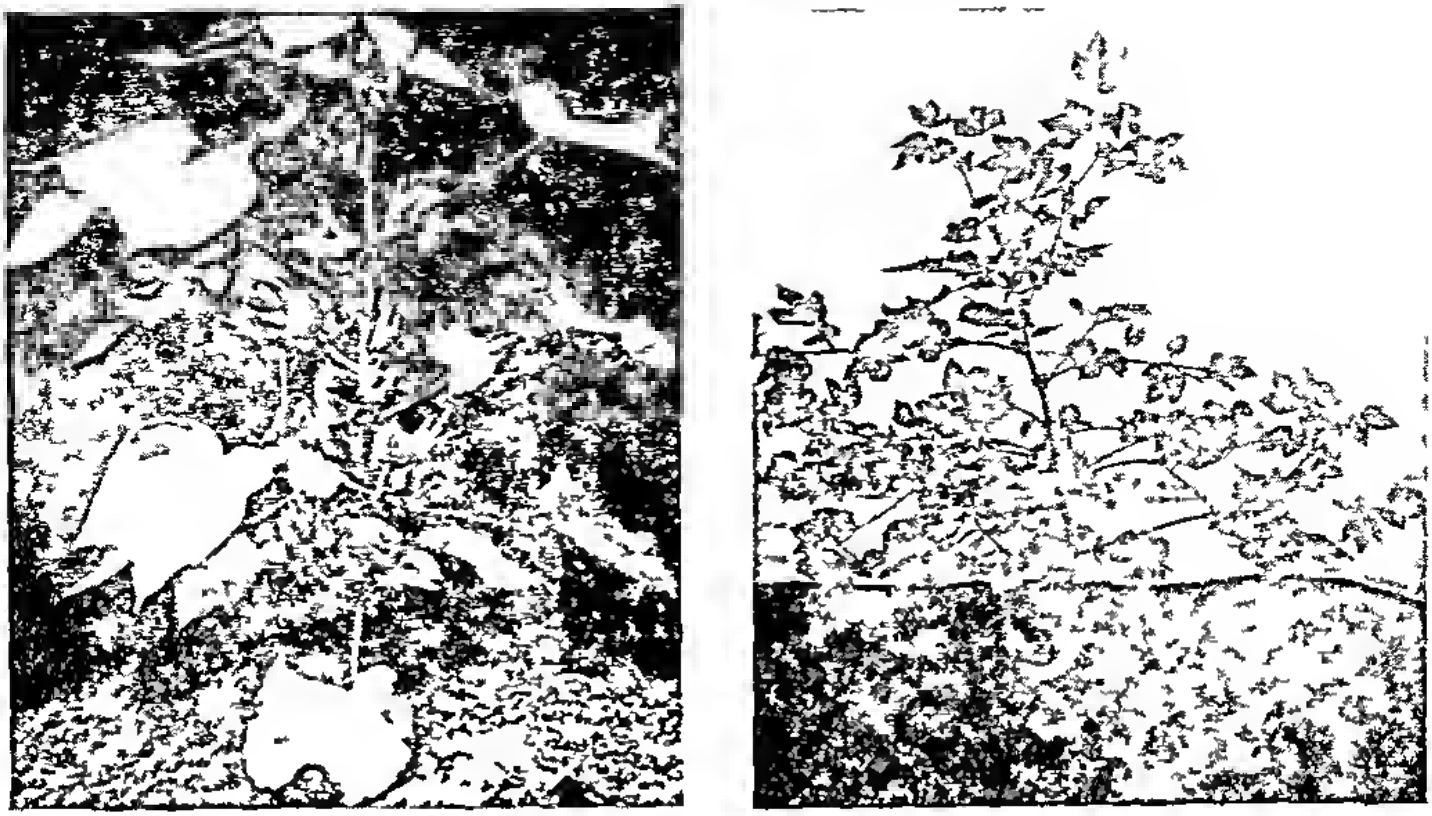
Principal objectives in the breeding of cotton are high production of lint fibre, early maturity, resistance to disease and insect injury, and improvement in fibre quality Other considerations are important in local areas

Yield of Lint Fibre. A high production of lint fibre is the ultimate objective in the breeding of cotton, if, of course, an acceptable quality of fibre is being produced The properties of good fibre quality will follow in a later topic The physical features that determine the yield of a cotton plant are the number of bolls, the size of the bolls, and the percentage of lint [47] High-yielding plants must be prolific and set a large number of bolls A large seed set is desirable since the lint is produced on the surface of the seed The density of the lint on the seed also affects the total lint production Lint density is a variety characteristic and may be improved by breeding Lint percentage, also referred to as ginning percentage or gin outturn, is weight of the lint expressed as a percentage of the weight of the seed cotton (lint and seed)

The percentage of lint determines the weight of the lint cotton that may be obtained from a given weight of seed cotton Size of seed is therefore associated with percentage of lint Large-seeded varieties normally have a low lint percentage, and small seeded varieties have a high lint percentage Size of seed is also generally associated with size of boll The size of the boll is measured by its weight and is usually expressed as the number of mature bolls to make one pound of seed cotton However, either large boll or small boll types may give high outturn, depending on the lint percentage. The *arboreum* varieties, Rosea 231 and Ganganagar, and the *herbaceum* variety, Digvijay, all have high lint percentage The Indian *hirsutum* variety, 134-Co 2-M, has large boll size. Boll weight is controlled by additive genes, and the possibility of improving boll number through heterosis has been suggested [31]

Normally, varieties that set a high percentage of five lock bolls are considered superior in yielding ability to varieties with four lock bolls The final yield of lint fibre is affected by the interrelation of all these characteristics, as well as disease and insect resistance, the loss in harvesting, and other factors

Another factor which contributes to yield is the stand or population of plants per unit area This has recently led to consideration of developing unbranched or short branched varieties which may be grown at higher plant populations per hectare



11 8A 11 8B

Fig 11 8 Comparison of short branched vs. long branched varieties of cotton A Short branched variety with bolls clustered around the main stem. B Long or open branched variety of Cambodia type Thicker stands may be grown using the short branched varieties, which may lead to higher yield.

of land area (Fig 11 8) A Russian variety, PRS 32 which has short branches and clustered boll habit, has been utilized in crosses with Indian varieties in Madras state from which short branched, erect strains have been isolated.[51]

Early Maturity. Early maturity in cotton has many advantages It enables the cotton crop to develop during periods of more favourable moisture and to be picked before damage from unfavourable whether Early maturity helps to fit the cotton crop into double cropping patterns. Losses from late disease and insect injury may be reduced by the use of early varieties The use of early and rapid fruiting types of cotton to escape damage from the boll weevil has long been practiced in America Earliness and uniform maturity are essential in areas where cotton is harvested mechanically Early maturity is desirable in irrigated areas as early maturing plants are more economical in use of irrigation water than late varieties

Earliness in cotton is not a character that can be easily measured since the cotton plant flowers and sets bolls over a long period of time Earliness is influenced by (*a*) how early the cotton plant begins to flower, (*b*) rate at which the flowers open, and (*c*) the length of time required for the boll to mature The relative length of these periods varies in different varieties as well as with environmental conditions in which the cotton plant is grown In a study on methods of measuring earliness in cotton it was concluded that the weights of the seed cotton obtained in the first and second picking expressed as a percentage of total seed cotton, was a good practical measure of earliness [45] Inheritance of the length of time from blooming to boll opening appears to be controlled by genes having additive effects. Characters which appear to be associated with earliness are small plant size, small seeds and bolls, and bolls set close to the ground The latter characters are undesirable to the grower if they result in lower yields or increase the difficulty of harvesting

Picking Quality Cotton is harvested by hand picking in Asian countries Large bolls and bolls that flare back on ripening are easy to pick by hand The fully exposed cotton may of course be damaged by storm or wind so the locks in the boll need to hold together rather firmly Uniform ripening makes picking more economical Freedom from spines on the bracts which may be injurious to the pickers' hands is desirable

Where mechanical pickers are used, boll size and opening do not form a dependable criteria for picking quality Bolls that open wide enough to permit the cotton to fluff so that it will be caught by the spindles are desirable, but it is also necessary that the varieties have sufficient storm resistance to cause the fibre to stick in the burr and not be blown or rained out before harvest A compact plant, with bolls spaced along the main stems and set high off the ground, is best suited for machine harvesting An early short fruiting period permits the plant to mature more of the bolls in a short space of time Smooth leaves free from hairs and small bracts reduce the trash in mechanically picked cotton

Disease Resistance. Many diseases attack the cotton plant In India breeding for resistance has been concentrated on two diseases, Fusarium wilt and bacterial blight or blackarm disease

A FUSARIUM WILT (*Fusarium oxysporum f vasinfectum*) Fusarium wilt is caused by a fungus that inhabits the soil [14] The water conducting tissues of the plant are damaged by the disease, and wilting of the plant and premature killing results (Fig 11 9) The disease is usually associated with injury caused by nematodes, which provide openings through which the wilt fungus enters the roots Breeding for resistance was started before 1900 A wilt resistant variety of Sea Island cotton Rivers, and two upland varieties Dillon and Dixie were developed in the U S A by selection of resistant plants growing on wilt infested soil [67] Seed harvested from the resistant plants was then tested on a progeny row basis In the breeding of these varieties the principles of survival and progeny testing were introduced to cotton breeding Various studies on the inheritance of the disease indicate the presence of two or three dominant genes controlling resistance to the wilt disease [58 67] Resistant varieties in India include H 420 and Virnar in *G arboreum*, K F T, Digvijay, and Jayawant in *G herbaceum*, and Co 2 in *G hirsutum* [52 56] The U S varieties Coker 100 Wilt, Stonewilt, and Auburn 56 are nematode resist-

Fig 11 9 Comparison of a Fusarium wilt susceptible variety, planted on wilt infested soil, with wilt resistant varieties on either side

ant besides being highly wilt resistant The resistance to nematodes reduces the nematode injury and hence the points of entry into the cotton roots for the wilt fungus [44] Resistance to wilt may be checked by growing plants in wilt infested soil in the field, or in pots or plastic bags in the glasshouse using soil to which cultures of the wilt organism have been added [73]

B BACTERIAL BLIGHT Bacterial blight also called blackarm angular leaf spot and boll blight, is a bacterial disease caused by *Xanthomonas malvacearum* The Indian *arboreum* and *herbaceum* varieties are not much affected by the disease but the American *hirsutum* cottons in India are highly susceptible Extensive studies on resistance have been carried out in Sudan, U S A , India and other countries

Ten genes have been identified for resistance to bacterial blight or blackarm [36 37] Two genes, B_3 and B_6 came from *G arboreum* One gene, B_8 came from *G herbaceum* Five genes, B_1 B_2 B_3 B_7 and B_{10} were identified in *G hirsutum* One gene B_5, was found in *G barbadense* One recessive gene, b_9, was found in *G anomalum* All of the genes except b_9 have been transferred to Sudan strains of the Sakel variety of *G barbadense* and several genes have been transferred to American Upland, *G hirsutum* The different genes confer different levels of resistance dependent upon the genetic background and the modifying genes present In a study of several crosses involving different gene combinations plants with the B_2B_6 combination were most resistant [27] The resistance genes identified conferred resistance to leaf infection [36] Certain of the genes which confer resistance to the leaf phase of the blackarm disease are not as effective in controlling the boll phase of the disease Plants may be artificially infected by spraying with inoculum containing the *Xanthomonas* organism [25] Plants are then graded on a scale of 0—immune to 12=susceptible,[36] or a scale of 0=immune to 7=susceptible is also used [49] In India resistant varieties have been developed from *hirsutum* × *herbaceum* crosses [4 52 56]

C OTHER DISEASES Root rot caused by *Rhizoctonia* sp , anthracnose caused by *Glomerella gossypii* red leaf blight and leaf curl diseases also cause damage to the cotton plant Few studies of resistance have been made with these diseases The varieties Co 2 in Madras and Laxmi in Mysore are reported to be resistant to red leaf blight [58]

Insect Resistance Considerable breeding work has been done on jassid or leafhopper resistance in Africa Australia and India and some work has been done on pink bollworm and thrip resistance

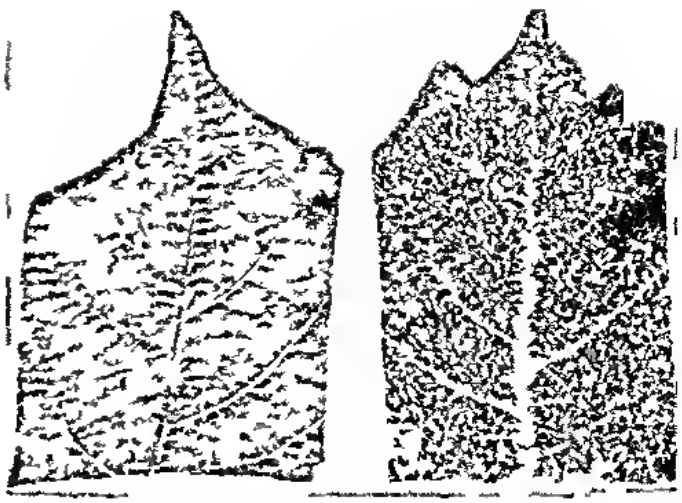


Fig 11 10 Comparison of hairiness of the leaf of two cotton varieties Hairy leaves give protection from the insect pest jassids

A JASSID RESISTANCE In India infestations on cotton due to jassids (*Empoasca devastans*) are most severe on the *hirsutum* varieties grown in the irrigated tracts [46] The *arboreum* and *herbaceum* varieties are more resistant owing to presence of dense hairs Failure of the early introductions of American upland varieties was in part due to their susceptibility to jassids [23] The presence of long and dense hairs on the lower surface of the leaves protects the cotton plant from jassid attack (Fig 11 10) Hence, resistant varieties have been developed by breeding for increased hairiness [35 51] It will be recalled that the current Punjab American varieties of *hirsutums* were selected from hairy plants that persisted in the fields of desi cottons and that the Cambodia *hirsutums* possessed a dense hair covering when introduced

Much work has been done on the genetics of hairiness of cotton, and 6 hairiness genes have been identified A major gene for leaf hairiness H_1 has been identified in the varieties Tanguis (Peru) and *Carpulla* (Ecuador) of *G barbadense*, the varieties Malwa Upland 8b (India), Cambodia UA7 29 (India), and Kawanda (Uganda) of *G hirsutum*, the variety Wagad 8 (India) of *G herbaceum*, and in *G anomalum* (Angola) The gene H_2 also a major gene for leaf hairiness has been identified in *G*

the spinner to spin yarn with uniform size and strength and with less waste Cotton breeders often refer to "halo length" with reference to staple length Halo length denotes the length of a small sample of fibres that are combed into a halo This provides the breeder with a quick method of estimating fibre length

B FIBRE STRENGTH High tensile strength of the fibre is necessary for good spinning properties Staple from varieties which produce weak fibres is difficult to handle in manufacturing processes The structure of the inner layers of the cotton fibres is a major factor in determining its tensile strength [3] Strength may be expressed as pounds required to break a bundle of fibres with a given cross sectional area The tensile strength of cotton fibres normally ranges between 70,000 and 90,000 pounds per square inch A machine, called the Pressley strength tester, has been devised to measure the strength of small samples of cotton fibres The stelometer is another machine used to measure fibre strength Cotton varieties differ markedly in fibre strength The *G barbadense* species is characterized as having strong fibre

Maturity is an important factor in fibre strength Varieties with uniform flowering contribute to uniform maturity of cotton fibre and hence uniformity in strength of the fibres

C FIBRE FINENESS Cotton fibres from some varieties feel soft and silky Fibres from other varieties feel coarse and harsh The difference in the way they feel is determined by the fineness or coarseness of the fibres Fibre fineness is associated with diameter of the fibre and with the thickness of the fibre wall When the fibres fail to develop an average amount of inner wall they are said to be 'immature" The Indian cotton technological laboratory has developed a simple quartz microbalance for measuring fibre weight Modern instruments like the Micronaire and Arealometer are also used to measure fineness of fibre The latter instruments measure the surface of a given weight of fibre by resistance to airflow [30] There is a considerable range of variability in fibre weight of cotton varieties in India. Strains have been developed with low fibre weight in the *hirsutum* group [56] Another measure of fineness and spinability of cotton fibre is the count of the yarn The count is the number of hanks of yarn which weighs one pound A hank consists of 840 yards of yarn Average warp counts for the species cultivated in India are *G arboreum*, 6 to 44, *G herbaceum* 8 to 43, *G hirsutum*, 14 to 56 [56]

D COTTON QUALITY TESTING LABORATORY A Technological Laboratory under the auspices of the Indian Central Cotton Committee was established at Bombay in 1924 The laboratory assists the cotton breeders, working in the different experimental stations throughout India, in evaluating the fibre qualities of their breeding materials In addition, cotton fibre specialists are attached to many of the cotton breeding stations in India

E GLANDLESS COTTONSEED Cotton seeds normally have darkly pigmented glands that contain a *toxic* substance called *gossypol* Nonruminant animals cannot ingest large amounts of cottonseed cake without showing ill effects due to the presence of gossypol Gossypol may be inactivated by heating or by chemical processes but this increases the cost of cottonseed cake Recent research in the U S A has been devoted to development of varieties of glandless cotton that will be free of gossypol Results indicate that oil from glandless cotton seed is lighter in colour and that cottonseed cake from glandless cotton gives higher gains when fed to poultry than cake from glanded cotton There appears to be preference by some insects for glandless cotton, a problem which needs further study Three genes have been identified which are involved in glandlessness and these have been designated $g^1 1$, $g^1 2$, and $g^1 3$ Combinations of $g^1 1$ and $g^1 2$ are required to condition the glandless character

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B PINK BOLLWORM The pink bollworm, *Platyedra gossypiella* Saund, causes much damage to cotton in India Resistance is reported in types of *G hirsutum* from Hawaii, *G thurberi*, *G raimondii*, *G somalense*, and *G armourianum*,[92] but little progress has been made in breeding for resistance

Fibre Quality. The value of the cotton crop comes from the commercial uses of cotton fibre In recent years competition with synthetic fibres and foreign grown cotton has increased As a result, improvement in the fibre properties of cotton has become an important objective with cotton breeders in India and elsewhere Recent advances in knowledge of fibre technology have made it possible for the breeder to measure the characteristics of the cotton fibre and to breed strains with properties desired by the spinner of cotton yarn and the manufacturer of cotton textiles [5 17 30]

Cotton fibre is borne in bolls consisting of three to five locks The fibres developing on the cotton seed may be separated into two groups according to length The outer layer, or *lint*, is composed of long fibres which are separated from the seed in ginning The inner layer, or *fuzz*, is composed of short fibres which remain attached to the seed after ginning The lint fibres are used in spinning cotton yarn The fuzz fibres are used in making rayon and other cellulose products

The individual fibre is borne on the seed and is an outgrowth of a single epidermal cell The cotton fibre cell is a thin walled tubular structure which elongates until it reaches its maximum length The tubular fibre cell is thickened by the deposition of cellulose on the inside [3] As more cellulose is deposited, the fibre wall becomes thicker, and the hollow core inside, or *lumen*, becomes smaller With reference to the cotton fibre, the term *maturity* is used to denote the stage of development of thickness in the fibre wall Immature fibres have thin walls, but as the fibre matures, the walls become thicker The elongation of the individual fibres occurs over a period of thirteen to twenty days, depending upon the variety and the environment A longer period is required for the elongation of the fibre in a long fibre variety than in a short fibre variety After elongation ceases, the cellulose is deposited in successive layers on the inner wall of the fibre over a period of twenty-five to forty days The structure of the inner wall, as determined by the manner in which the cellulose is deposited, largely determines the spinning properties of the lint fibre This varies with the variety, although it, too, may be modified by the environment

Fibre quality is judged by its spinning value or spinability, which in turn depends upon various physical properties of the fibre The most important of these properties are *fibre length*, *fibre strength* and *fibre weight*

A FIBRE LENGTH Fibre length, also called staple length or lint length, is the normal length of a typical portion of the fibres of a cotton sample It is traditionally stated in gradations of thirty-seconds of an inch The *arboreum* and *herbaceum* species in India are short staple varieties averaging less than one inch while *hirsutum* averages from one inch to 1 1/32 inches in staple length Measurements of fibre length may be made by sorting a sample of cotton fibre into various length classes and measuring each This may be done with a machine called the Balls Sorter A more rapid method of evaluating fibre length has been developed in the U S A which uses an electronically regulated optical instrument called the Fibrograph [30] The Fibrograph measures the mean length and the upper half mean The *mean length* is the average length of all the fibres The *upper half mean* is the average length of the longer half of the fibres, a measurement which compares roughly with staple length A *uniformity ratio* for fibre length is (mean length $\times 100$)/(upper half mean) The uniformity ratio in cotton varieties usually varies from 70 to 90, with the more uniform samples giving the higher ratios [17] Uniformity of staple length is related to the spinning behaviour and utility of the cotton Fibre length is highly correlated with the strength of the yarn Considerable variation in the length of the cotton fibres may be found within a variety and even within a single boll Uniform staple length in a variety enables

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12

Breeding Sugarcane

Sugarcane is widely grown in the tropical and subtropical areas of the world, and is an important crop in all of the countries of tropical Asia In India, sugarcane occupies about 2 1/2 million hectares, cultivated mostly in the subtropical belt across north India from Assam to Punjab, with about one half of the total acreage in the state of Uttar Pradesh The production of sugarcane in north India, rather than in the more tropical areas of south India, is due partly to heavier soils more favourable for sugarcane production than the sandy soils of south India, and partly to the fact that indigenous types adapted to growing in that area of India have been cultivated there since very early times

SPECIES OF SUGARCANE

Sugarcane belongs to the genus *Saccharum* in the family *Gramineae* There are three species of cultivated sugarcane within the genus *Saccharum* (*S officinarum*, *S sinense* and *S barberi*) and two wild species (*S robustum* and *S spontaneum*) (Fig 12 1) While there are several other species of *Saccharum*, they have little or no sugar and can scarcely be regarded as sugarcanes [9 59] Present sugarcane clones in cultivation are mostly complex hybrids among these species and it would be difficult to classify them into any particular species

Saccharum officinarum. This species includes the tropical, "noble" canes indigenous to the New Guinea region [59] They are characterized by thick stems, soft rind, high cane yield or tonnage, low fibre, and high sugar content Originally they were grown by the natives in the New Guinea region as garden or chewing canes and for centuries were the only cultivated canes in the tropical regions of the South Pacific They include such historically famous commercial canes as Bourbon, Cheribon, and Tanna or Caledonia The term "noble" was applied to the tall, handsome, large barrelled, colourful canes of this species by the Dutch research workers in Java The canes of *officinarum* do not withstand well the rigours of drought or occasional frost, such as occur in the semitropical climates of north India or north Burma, and so have never been commercially important in that area although they may be

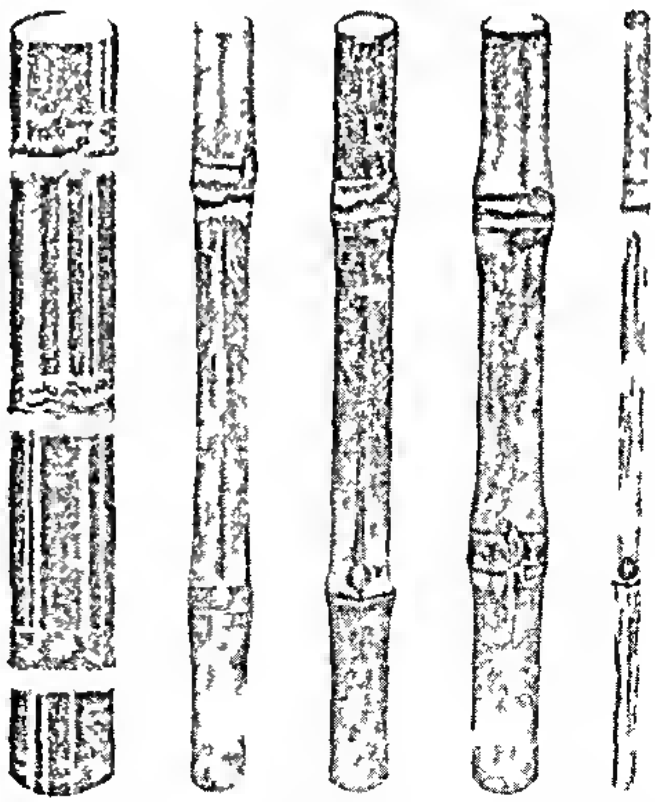

Fig 12 1 Canes of the cultivated and wild species of sugar cane A *S officinarum* (noble cane), B *S barberi* (north Indian cane), C *S sinense* (Chinese cane), D *S robustum* (wild cane), E *S spontaneum* (wild cane)

grown occasionally as chewing canes Canes of *officinarum* are generally resistant to smut, but are highly susceptible to the diseases red rot and mosaic Outbreaks of these diseases virtually eliminated *officinarum* species from large scale commercial production In recent years the *original noble* canes have been succeeded in cultivation by complex hybrids among *officinarum*, *spontaneum*, and other species

S. sinense and S. barberi. These species may be considered together since they are similar in all important respects They are indigenous to north India, East Pakistan and the Burma China region Barber, working in India classified the indigenous orth Indian canes into five groups, Saretha, Sun nabile, Nargori, Mungo, and Pansah, based on morphological characteristics of the stem, roots, and leaves, and included all of them in the species, *S sinense* [7] Later Jesweit, a Dutch worker in Java, placed the first four groups of varieties into a new species, *S barberi*, but retained the Pansah group in the species *S sinense* This grouping is still widely used However, Artschwager,[4] after studying clones of the Indian canes in the U S A , suggests that the division into the two species is not justified and reats all of the north Indian canes as belonging to *sinense*, a view that is also held by Price [44]

The canes of these species are characterized by thin stalks, great vigour, early maturity, and wide adaptability They can withstand light frost and drought, characteristics which adapt them for cultivation in northern India. They are poor in cane yield, intermediate to low in sugar content, resistant to the red rot disease susceptible to smut, and vary according to the clone from susceptible to immune for mosaic disease The sugar production in north India depended on the canes of this origin for many centuries, but currently canes of these species have been replaced in cultivation by complex hybrid clones Canes of the Saretha group have been used most successfully for breeding improved varieties [59]

S. spontaneum. The clones of the wild species, *spontaneum*, form a complex group with great diversity and with much natural hardiness [9 40 59] The species is found in India, southwest Asia, southeast sia, China, Taiwan the Philippines, the South acific islands, and tropical Africa. In general, the orms of this species are perennial, have slender talks, high tillering capacity, high fibre, and low sucrose content Clones of *S spontaneum* are available which are resistant to sereh, mosaic red rot, and Pythium root rot, but all are susceptible to smut [9 36] A collection of about 400 forms of *S spontaneum* is being maintained at the Sugarcane Breeding Institute, Coimbatore About 100 of these collections are from outside India *S spontaneum* is widely used in the breeding of new hybrid clones to contribute genes for vigour, hardiness, tillering capacity, and disease resistance

S. robustum *S robustum* is a wild species discovered in New Guinea in 1928 [79] The species has great vigour and wide adaptability The canes are tall with medium thickness, high fibre, and low sucrose content They are susceptible to mosaic

Related Genera. Related genera which may be useful in the breeding of sugarcane are *Erianthus*, *Sclerostachya Narenga* and *Sorghum* [30 52] While inter generic crosses have been successfully accomplished between sugarcane and each of these genera, none of the hybrids have so far entered into the production of a commercial clone

ORIGIN OF SUGARCANE

The cultivated sugarcanes had two geographic centres of origin, New Guinea, and northern India [13 39] The large barrelled, tropical species, *S officinarum*, probably originated from the wild species, *S robustum* in the New Guinea region [14 13 29] As it migrated outward from its centre of origin, it became modified by natural hybridization with a species of a related genus, either *Erianthus maximus* [11 29] or *Sclerostachya fusca* [43] The north Indian sugarcanes, *S sinense* and *S barberi* are believed to have originated in northern India by natural hybridization between migrating forms of *S officinarum* and wild *S spontaneum* [42] This origin presupposes that the presence of *S officinaeum* in the India Burma region antedates the origin of the north Indian species

CYTOGENETICS

The *Saccharum* species are extremely complex polyploids with high chromosome numbers [15 16] The chromosome number as reported by different workers may vary with the particular clone studied The chromosome number may be modified by the appearance of aneuploids within the species, as well as by gains or losses due to simple meiotic irregularities Chromosome numbers most commonly

reported for the *Saccharum* species and a few species from related genera are as follows [10 41 45]

S officinarum	$2n = 80$
S barberi (Saretha group)	$2n = 90, 92$
(Sunnabile group)	$2n = 82, 116$
(Nargori group)	$2n = 107, 124$
(Mungo group)	$2n = 82$
S sinense (Pansah group)	$2n = 116, 118$
S spontaneum	$2n = 40$ to 128
S robustum	$2n = 60$ to 148
Erianthus maximus	$2n = 60$ to 100
Sclerostachya fusca	$2n = 30$
Narenga porphyrocoma	$2n = 30$

The most common basic chromosome numbers are 8 and 10 [10 38 44] *Saccharum officinarum* is considered to be an octoploid with a basic number of 10 In the wild species *S spontaneum*, there appears to be two polyploid groups One group in this species has a basic chromosome number of 8 and $2n$ chromosome numbers of 40, 48 56, 64, 72, 80 96, 104 112, 120 and 128 [10] The other group has a basic chromosome number of 10, with $2n$ chromosome numbers of 40 50, 60, 70, 80 100 and 120 The other wild species, *S robustum* probably has a basic chromosome number of 10, with $2n$ number of 60 and 80 being most common,[10 45] although 84 chromosomes have also been reported, as well as a basic number of 8 [10] All of this emphasizes the complexity of the cytogenetics of the sugarcane species, which are highly polyploid and tolerant of various aneuploid combinations

Interspecific crosses can usually be made among the five species of sugarcane within the genus *Saccharum* although some peculiar chromosome numbers are observed in the progenies of certain *Saccharum* interspecific crosses [10 14] Due to some abnormality in the process of fertilization and embryo formation, the somatic chromosome number instead of the gametic number of the pistillate parent is transmitted to the progeny when *S officinarum* is used as the maternal parent in crosses with *S spontaneum*, *S barberi*, or *S sinense* For example in crosses of *S officinarum* ($n = 40$) as the maternal parent with the wild species *S spontaneum* ($n = 56$) as the pollinator, the hybrid, instead of the normal chromosome number of $40 + 56$, will contain $40 + 40 + 56$ or $2n = 136$ chromosomes If the hybrid ($n = 68$) is backcrossed with the *officinarum* parent type ($n = 40$) as the maternal parent, the BC_1 will have $40 + 40 + 68$, or $2n = 148$ chromosomes Additional backcrosses do not result in further increases in chromosome numbers This phenomenon does not normally occur when *S officinarum* is used as the pollen parent The probable chromosome constitution of F_1 progenies in interspecific crosses is shown schematically by the following [10]

Cross	*Chromosomes in* F_1
S officinarum × *S spontaneum*	$2n + n$
S officinarum × *S barberi*	$2n + n$
S officinarum × *S sinense*	$2n + n$
S officinarum × *S robustum*	$n + n$
S spontaneum × *S officinarum*	$n + n$
S barberi × *S officinarum*	$n + n$
S sinense × *S officinarum*	$n + n$
S robustum × *S officinarum*	$n + n$

Exceptions will be found when particular clones within the species are utilized in the crosses

In the breeding of sugarcane, it has been a general practice to cross the noble cane, *S officinarum*, with other species in order to combine the high yield of sugar of the *officinarum* clones with hardiness and disease resistance of the other species This process in sugarcane breeding circles has acquired the term "noblization' Usually two or three backcrosses, or 'noblizations", may be made to the *officinarum* parent in order to recover satisfactory sucrose content and other desirable qualities of the noble parent

Genetic studies in the sugarcane have been rather meagre This is due to the high polyploid number, the heteroploid chromosome constitution of many varieties, and the difficulties involved in selfing and crossing [10 47 48] The genetic studies made have dealt mainly with morphological or other qualitative characters Very little is known about inheritance of economic characters such as maturity or disease resistance

VARIETIES

The term "variety" in cultivated sugarcane refers to a particular clone which is perpetuated by vegetative propagation from seedcanes or

The vegetative characteristics of the more important clones in commercial cultivation are generally described in detail and these descriptions may be used as the basis for future identification of the clone [3 5 7 24] In India, descriptions and agricultural characteristics of canes developed at the Sugarcane Breeding Institute Coimbatore have been published[53] with botanical descriptions based on the following information,

(*a*) parentage
(*b*) habit and general appearance
(*c*) leaf characters (lamina, sheath, blade joint arrangement)
(*d*) cane (colour, internode node bud)
(*e*) germination and seedling habit
(*f*) sett and shoot roots
(*g*) adult root system
(*h*) stem epidermal pattern

Naming Varieties. It has been the practice in sugarcane breeding stations throughout the world to identify improved sugarcane clones by letters to identify the sugarcane breeding station where the clone was selected, the letters to be followed by a number to identify the clone An example is Co 205 The letters Co stand for Coimbatore the city in India where the Sugarcane Breeding Institute is located, and 205 identifies this specific clone bred at the Coimbatore Station

Letters identifying clones from some of the principal sugarcane breeding stations throughout the world are as follows

Symbol	*Breeding Station*
B	Central Sugar Cane Breeding Station, Barbados, British West Indies
Co	Sugarcane Breeding Institute, Coimbatore, India
C P	United States Department of Agriculture, Canal Point, Florida
H	Hawaiian Sugar Planters' Association, Honolulu, Hawaii
M	Mauritius Sugar Industry Research Institute, Reduit, Mauritius
N	South African Sugar Association, Natal, South Africa
P O J	Java Sugar Experiment Station, Pasuruar, Java
Q	Bureau of Sugar Experiment Stations, Brisbane, Queensland, Australia

Modern sugarcane breeding was started in 1887 when it was discovered in Java that crosses between sugarcane varieties would produce viable seed Since then many varieties have been developed at sugarcane breeding stations in the principal sugar cane growing areas of the world A few of the outstanding clones or varieties that have been produced are as follows [9 12 23 59]

Australia Pindar, Q 57, Trojan

Barbados B 34104, B 37161, B 41227 B 4362, B 4744, B 49119 B 54142

Hawaii H 37 1933, H 44 3098 H 50 7209, H 49 5

India Co 205, Co 312 Co 419, Co 421, Co 453, Co 740

Java P O J 2878, P O J 3016 P O J 3067

U S A C P 44 101 C P 29-116, C P 48 103, C P 41-223 C P 50 28, C P 52 68, C P 55 30

When sugarcane breeding was first started in India in the early part of this century, about 100 varieties were being grown in the subtropical belt from Assam to Punjab [7] Many notable varieties have since been developed in India, mainly originating from interspecific crosses made at the Sugarcane Breeding Institute, Coimbatore The student will need to consult the Agricultural Department, or the Agricultural College or Agricultural University in his state to learn the varieties or clones that are best adapted to his area

Variety Decline. It has long been observed that sugarcane varieties tend to "run out" or decline in yield after being grown for a few years in a particular area To maintain high yields it has been necessary to replace varieties every few years with new clones This has been particularly difficult to understand from a genetic standpoint because the sugarcane variety is clonally propagated and is not expected to undergo genetic change as might conceivably occur in a seed propagated crop by mixing or through genetic segregation Neither do somatic mutations in the sugarcane appear to occur with sufficient frequency to be important in the decline in varietal performance While the exact cause of variety deterioration and yield decline has not always been determined with certainty, the explanation given most frequently is change in disease patterns An increase in a new disease, or

the evolution of new forms of an old disease to which the variety is not resistant may result in the failure of the variety to produce as abundantly as it did in the past [8 31 34] The Bourbon cane failed in Hawaii after 50 years of successful production due to increases in root diseases The same variety succumbed in Antigua from a rind fungus [8] *Pythium* root rot ratoon stunting disease red rot mosaic and nematodes have all been cited at different times as causes for varietal decline [9] The multiplicity of organisms in the soil which attack the roots of the sugarcane plant are capable of undergoing progressive changes which enable them to attack varieties previously resistant and productive This has required a continuous flow of new varieties from the breeder in order to maintain resistant and productive types in the field

BOTANY OF SUGARCANE

The commercial utilization of sugarcane is based on its abil ty to store large quantities of juice con taining sucrose in the stem Size of plant is therefore important as thick and tall stems can store more juice than thin or short stems and tonnage of canes is one criterion of sugar yield per acre Lateral buds which are able to germinate and form shoots and roots are found at the nodes of the sugarcane stem one bud to each node (Fig 2 11) Sugarcane is propagated vegetatively by stem cuttings called *setts* or *seedcanes*, having one or more buds Each bud may develop into a primary stem from which in turn develop secondary stems or tillers The leaves may be loose on the stems and break away easily in which case they are said to be *free trashing* or the leaf sheaths may adhere tightly The latter is undesirable as they hold water in wet weather permitting the root primordia to develop aerial roots Also the leafy material makes sugar process ing more difficult and more expensive owing to impurities getting into the juice

Sugarcane flowers sparsely except in the tropical areas Flowering in sugarcane is affected by the ecological situation Warm nights humid condi tions and high rainfall favours flowering while cool weather and high altitude inhibits flowering The flowering response also differs with the genotype of the clone For example clones of *S spontaneum* generally flower under a wide range of climatic conditions Flowering is undesirable in commercial canes as the plant stops growing and matures rapidly after the appearance of the flowering stalk or arrow However flowering and the capacity to produce fertile pollen and true seeds are important and necessary in breeding sugarcane in order to obtain genetic recombination

The sugarcane inflorescence consists of an open branched panicle known as an *arrow* (Fig 12 2), and may contain as many as 100 000 flowers The flowers are borne in paired spikelets one sessile and one pedicellate (Fig 12 3) [6 21 27] The flowers open in early morning usually between 5 and 6 A M About 7 to 14 days are required for an arrow to complete flowering The flowering starts at the top of the arrow and proceeds downward Cross pollination normally occurs

Sugarcane flowers show a wide range of fertility and seed production from male sterility to high pollen productivity and from self sterility to com plete self fertility The self sterility is presumably due to the presence of self sterility alleles The seeds produced are extremely small in size and often poorly developed and inviable The seeds and floral structures including the long silken hairs at

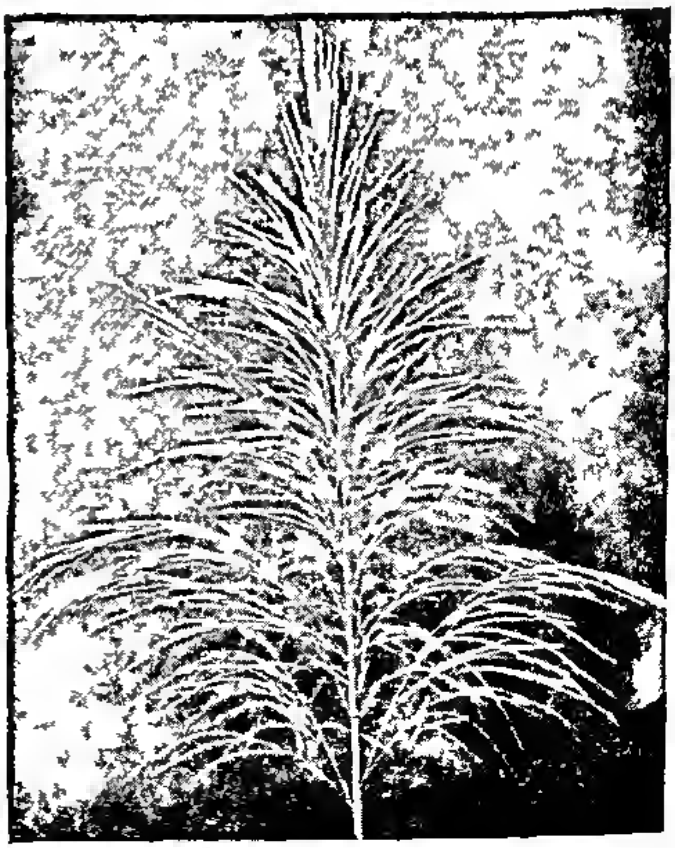

Fig 12 2 Flowering arrow of sugarcane plant

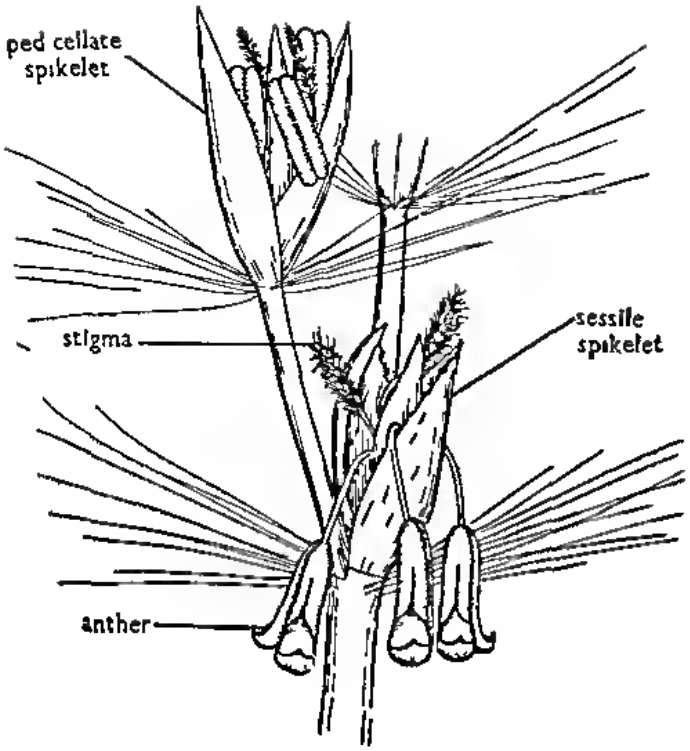

Fig 12 3 Part of inflorescence of sugarcane plant showing sessile and pedicellate spikelets The sessile spikelet flowers before the pedicellate spikelet

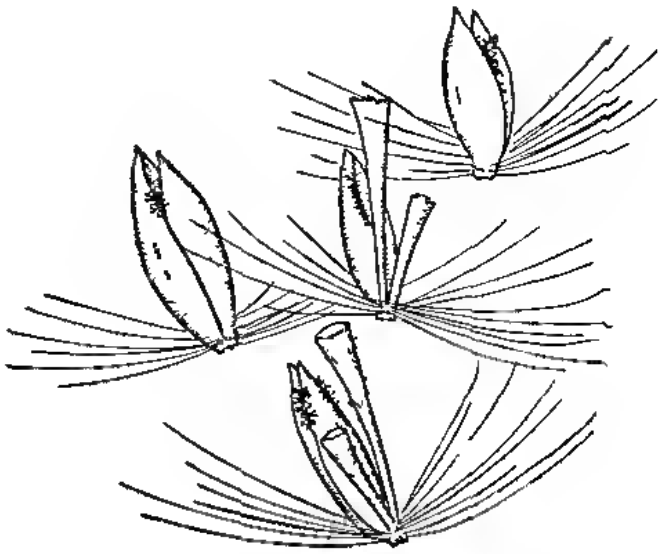

Fig 12 4 Fuzz or true seeds of sugarcane The stalk of the pedicellate spikelet and a rachis segment remains attached to the sessile spikelet The pedicellate spikelet breaks free The long silky hairs at the base permit the wind to carry the seed for long distances

the base of the spikelets, are generally referred to as *fuzz* or *fluff* (Fig 12 4) The fuzz breaks off easily and may be carried away by the wind In breeding experiments care must be taken to prevent loss of the seed in this manner

Selfing and Crossing Techniques. Selfing may be ensured and cross pollination prevented by covering the arrow with a bamboo frame work or cage and the cage covered with a closely woven cloth or a polyethylene bag forming what is commonly called a lantern (Fig 12 5) The temperature within the lantern may get rather high during midday so the bags are sometimes opened between noon and 4 00 P M when pollen dispersal is at a minimum in order to reduce the temperature inside Shading also helps to keep down the temperature within the lantern When lanterns are placed over the arrows in the field, a bamboo pole or scaffolding is needed to support the lantern

Cross pollinations may be obtained by isolating the parent lines from fertilization with foreign pollen, by enclosing arrows of the parent lines within a lantern, or pollen may be collected from the male parent and dusted over the arrow of the female parent. The crossing procedures may be done either with the arrows attached to the parent plants or with the arrows severed and transported to a central crossing area and maintained in a living condition by means to be discussed later Due to the small size and large number of sugarcane flowers on an arrow emasculation is not practicable When the arrows of the two parents are enclosed within the same lantern shaking the arrows occasionally may help to disseminate the pollen With artificial pollinations arrows shedding pollen may be dusted over the female parent, or arrows from the male parent are sometimes collected about 4 A M and brought into the laboratory where they are spread on paper and exposed to light at normal temperature. The pollen is shed on the paper and remains viable for several hours The flowers open between 5 and 6 A M and the pollen is dusted over the female parent arrows soon afterward Seedlings from selfed plants can sometimes be recognized from morphological characteristics and, in certain crosses, by checking chromosome numbers in the seedlings Pollen remains viable for several hours but some success has been attained with experimental studies on extending the life of the pollen by vacuum drying [19]

Cross pollinations performed by the above methods while the arrows still remain attached to tall plants growing in the field are both difficult and laborious Bamboo poles must be erected to

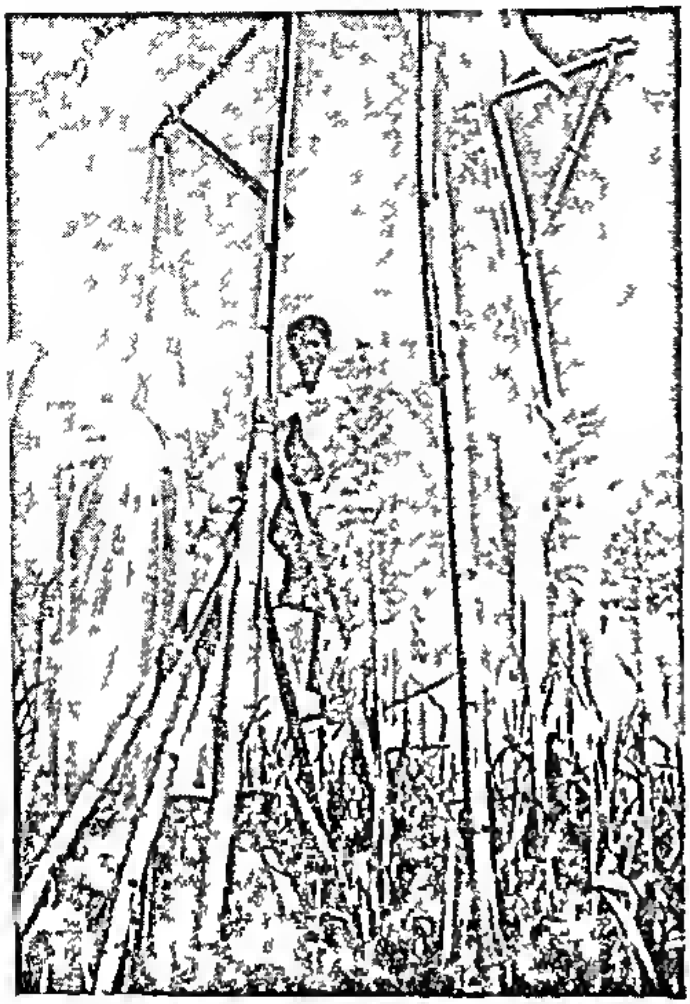

Fig 12 5 Bagging sugarcane plants in the field to prevent natural cross pollination A bamboo cage covered by a polyethylene bag is placed over the arrow to form what is called a lantern The lanterns are supported by bamboo poles

support the lanterns and ladders constructed so that the breeder can reach the arrow (Fig 12 5) Since an arrow normally flowers over a period of 5 to 10 days the pollination processes must be repeated daily during the period of flowering Arrows enclosed in lanterns yield fewer seeds than from open pollinations in the field Crossing by enclosing male and female arrows in a common lantern is limited to parent varieties planted in close proximity to each other To overcome these difficulties various modified procedures have been adopted by sugarcane breeders [17 22 23 32 33 64] These include transportation of arrows to a central crossing area where the pollinations are made extending the longevity of the severed arrows for several weeks mass crossing control of flowering and utilization of improved methods for seed storage

A USING DETACHED ARROWS To relieve the difficulties encountered in pollinating and bagging sugarcane arrows growing individually on tall canes it is the practice to sever the arrow from the base of the cane and transport it to a central crossing area This procedure was facilitated when it was learned that a detached arrow could be kept alive by immersing the cut end in a weak sulphur dioxide solution [33 62] or by marcotting [37] These techniques are now widely used at sugarcane breeding stations The tassels continue to bloom in the normal manner and remain alive for three to four weeks until the seeds mature

The practice of keeping alive the detached arrows in a weak acid solution was developed at the *Hawaiian Sugar Planters Experiment Station* [62 67] The severed sugarcane stalks are transported to a central crossing area where they are supported in an upright position with the cut end immersed in a solution containing 150 p p m SO_2 75 p p m H_3PO_4 37 1/2 p p m H_2SO_4 and 37 1/2 p p m HNO_4 The solution is changed and a fresh solution added at least biweekly

The marcotting procedure is fairly simple Just prior to flowering a polyethylene strip containing a mixture of moist potting soil is wrapped around a bud of the sugarcane stalk about 2 nodes above the ground level (Fig 12 6) Roots will develop on the stalk within a 10 day period where the bud has been marcotted Marcotted stalks are then severed and taken to the crossing area where the roots are placed in soil or in large sand mounds in a shady place Clusters of 3 or 4 arrows which are to be pollinated with the same pollen may be covered with a polyethylene hood or lantern At Coimbatore groups of hoods in the crossing area are surrounded and covered with a gunny or hessian cloth curtain (Fig 12 7) Both the sand mounds covering the roots and the hessian cloth curtain surrounding the hoods are sprinkled frequently throughout the day to keep down the temperature in the root zone and to keep up the humidity surrounding the arrows [37] The sugarcane plant requires about ten days to flower after showing signs of arrowing so plants do not need to be marcotted until it is clearly observed that they are going to arrow Since many stalks do not flower this economizes on labour by making unnecessary the marcotting of large numbers of stalks that may never flower

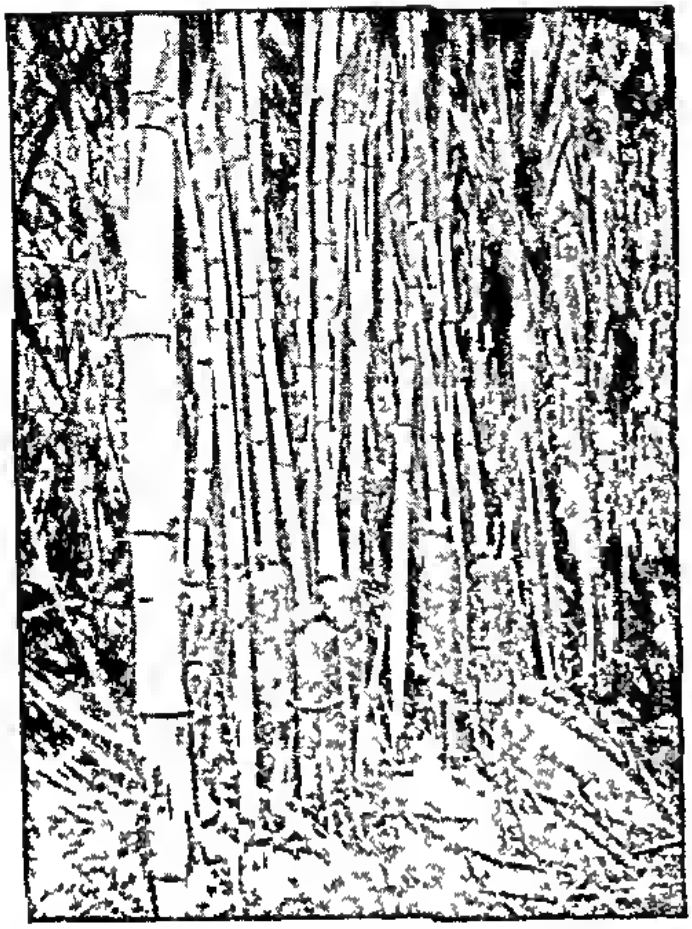

Fig 12 6 Marcotted stalks of sugarcane A polyethylene strip containing a soil mixture is wrapped around the node of the sugarcane stalk The stalk will root within a 10 day period

Pollination of arrows on stalks maintained in solution, or on marcotted stalks, may be done either by enclosing male and female arrows under the same hood, or by dusting the arrows of the female parent with pollen collected as previously described At Coimbatore, seed setting is generally better when pollen is dusted over the flowers daily, a process called "pollen loading", than when male and female arrows are included in the same hood or lantern Isolated crossing areas may be set up where all of the arrows are to be pollinated with a common male parent, or where free interpollination of clones within the crossing area is permitted It is then unnecessary to enclose the arrows in a hood, provided of course that the isolation of the crossing area is adequate to exclude foreign pollen After the arrows have completed blooming, the arrows from isolated crossing areas may be transported to a "central ripening area" where they can be maintained and watched more efficiently until the seed is harvested

B SYNCHRONIZATION OF FLOWERING Flower initiation in sugarcane, as in other crops, is affected by response to the photoperiod The time of flowering of native clones of *S spontaneum* collected in India between latitudes of 5 to 35 degrees north varied with the latitude at which they were collected [41] In general, moving the clones northward caused flowering to be delayed and moving them southward caused flowering to be hastened

Attempts to synchronize flowering in parent clones of sugarcane to facilitate crossing have been centred around (*a*) induction of flowering in non flowering clones (*b*) delay of flowering in early flowering clones, and (*c*) hastening of flowering in late flowering clones Various procedures have been attempted including alternation of photoperiod, adjustment of temperature geotropism and use of chemicals Adjustment of photoperiod and temperature have been the most successful practices although there is no complete agreement on the best procedure [21 28 32 63]

At Coimbatore, in south India, it has generally been possible to induce flowering in nonflowering clones or to hasten flowering in late flowering clones by reducing the length of the period of daylight and to delay flowering and continue the vegetative period in early flowering clones by increasing the period of daylength The problem is to know when and how long to give the extra light or to withhold the daylight Different clones will vary in this respect and must be studied individually Clones normally planted in February at Coimbatore flower in October or November and the change from the vegetative to the reproductive phase is initiated sometime between June and September To influence the flowering behaviour the light or dark treatments are given in advance of this period Other procedures used are the shortening of the daylight period gradually to induce flowering and the interruption of the dark period with a short light period to prevent flowering

C CARE OF SEED The seed or fuzz (Fig 12 4) is harvested when ripe, which will be about three weeks following pollination, dried, and stored Seeds may be planted immediately after being harvested and dried Sugarcane seeds retain their viability only for a very short period of time under normal storage temperatures, the viability often being re-

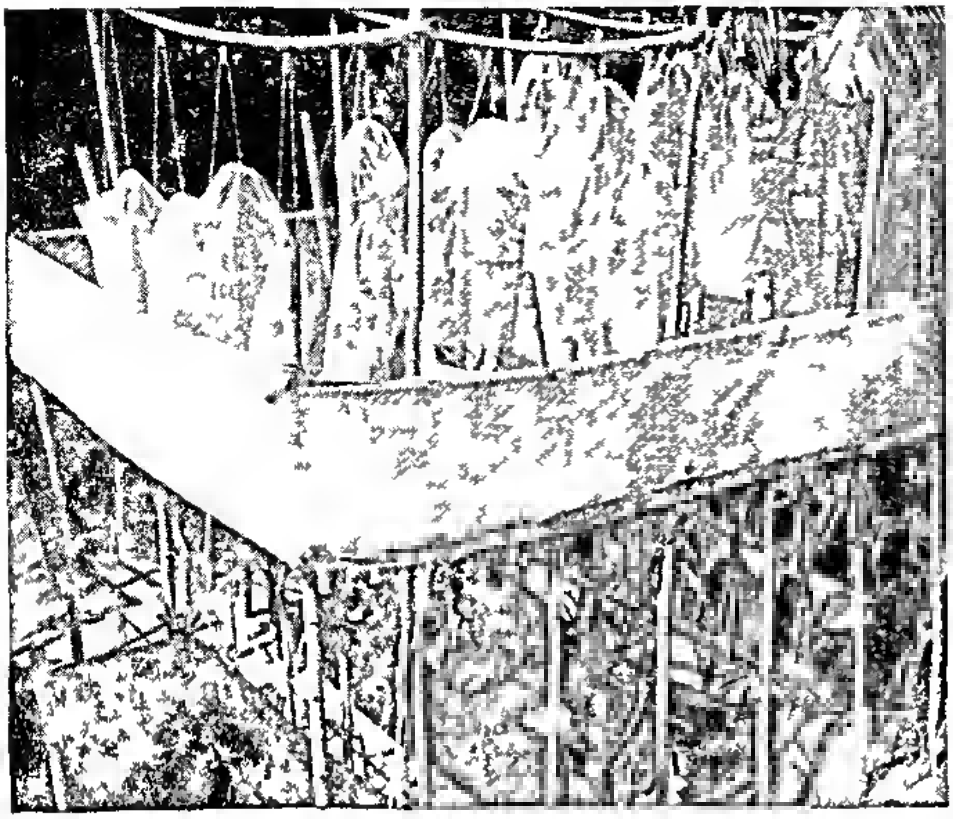

Fig 12 7 Groups of hoods or lanterns surrounded by a hessian cloth at the Sugarcane Breeding Institute Coimbatore The sugarcane stalks bearing the arrows have previously been marcotted as shown in Fig 12 6

duced by as much as 50 per cent within 30 days after maturity However, the life of the seeds may be extended to several years by storage at temperatures of 0 to 5 degrees Centigrade If dry the seed may be stored at temperatures below freezing

METHODS OF BREEDING

Methods of breeding sugarcane are based on the following considerations (*a*) The sugarcane plant is a complex polyploid and is highly heterozygous (*b*) The sugarcane plant does not flower freely except in favourable climatic locations, or if it flowers it may not set seed (*c*) Male sterility or incompatibility may be present (*d*) Sugarcane clones may be propagated vegetatively by means of stem cuttings or setts In common with other vegetatively propagated crops, clonal selection and hybridization have been the principal breeding procedures, with introduction playing an important role in supplying sources of breeding materials

Introduction and Germ Plasm Collection. The indigenous sugarcanes of north India, belonging to the species *S barberi* and *S sinense*, are thin-stemmed and low in sugar content The noble canes of *S officinarum*, indigenous to the New Guinea region, are less tolerant to frost and drought and are grown in northern India only on limited acreages as chewing canes They have been grown to some extent in south India and have been used extensively in crosses with the indigenous canes of India Most of the clones presently grown commercially in India are complex hybrids involving indigenous canes, introduced canes of *S officinarum* or *S robustum*, and clones of the wild *S spontaneum*

The Sugarcane Breeding Institute, at Coimbatore and Cannanore (Kerala State), and the United States Department of Agriculture at Canal Point, Florida, in the U S A , are maintaining large world collections of sugarcane clones [25] Over 2,000 clones are included in the collection at Coimbatore Of the clones being maintained about one half are hybrids developed at Coimbatore or elsewhere in India, and the remainder are clones of various species or foreign commercial hybrids Nearly 700 clones are *S officinarum* Special attention has been given to assembling clones of the wild *S spontaneum* species [40] Much of the current breeding work with sugarcane in India involves production of complex hybrids which contain genes from this wild species (Fig 12 8) [13 51] Formerly a large collection of canes was maintained at the sugarcane breeding station in east Java

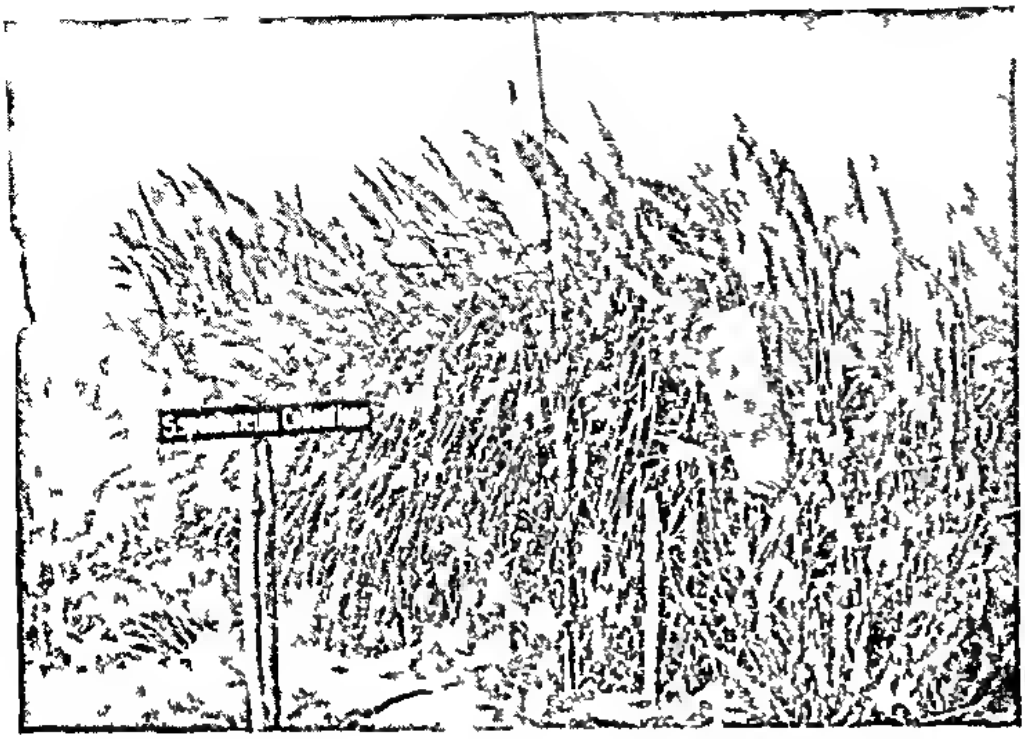

Fig 12 8 Collection of the wild sugarcane species *S spontaneum* maintained at the Sugarcane Research Institute Coimbatore *S spontaneum* is used in breeding for hardiness and disease resistance

Clonal Selection Clonal selection is used to isolate desirable clones from genetically mixed populations The mixed populations may be native or unimproved populations, inbred populations, or hybrid populations Since wild or unimproved populations will usually be mixtures of heterozygous clones it may be possible to isolate clones superior for particular characteristics which can then be used for breeding The wild *S spontaneum* collection at Coimbatore is being screened to locate clones with desirable agronomic characters or with disease resistance Since *S spontaneum is not suitable* to be entered directly into cultivation genes for the superior qualities would need to be transferred to commercially acceptable clones by hybridization procedures There is slight chance that selection within an improved variety established by setts as a single clone would yield an improved type since genetic variation in such a clone could result only for somatic mutation

Inbreeding has been used to concentrate genes for desirable characters of a quantitative character such as sugar content, in sugarcane varieties [20 57 58] It may also be used to increase homozygosity of genes for more simply inherited characters although the polyploid nature of sugarcane renders this more difficult than in a low polyploid species Inbreeding usually accompanied with *loss of vigour and* fertility but this need not always be the case [58] It is more probable that clones selected following inbreeding will be used as parents in the further production of hybrids than for direct cultivation Vigour lost in the inbreeding may be restored by this outcrossing

The most fruitful populations for clonal selection are the hybrid populations created by the breeder by careful choice of parent varieties

Hybridization Hybridization between clones followed by clonal selection within the hybrid *population is the procedure by which sugarcane* varieties are commonly developed [32 49 59] Since the sugarcane plant is heterozygous segregation will occur within the F_1 generation In practice crosses are made freely and several thousand seedlings may be grown from a single cross The breeding value of the parents is assessed by the performance of the progeny If a cross is found to have desirable seedlings in the progeny it may be repeated If a clone is found to contribute desirable characteristics to a series of progenies in other words if it shows good general combining ability it may be used in a large number of crosses

A HYBRIDIZATION PROCEDURES Several types of crosses may be made in the breeding of sugarcane [33] While these involve common principles the terminology and the procedures used may be considered

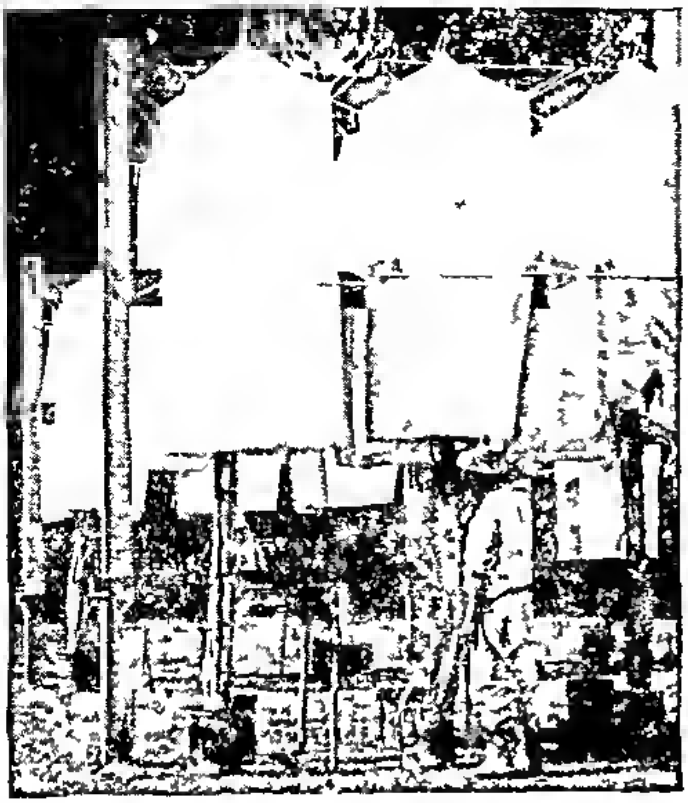

Fig 12 9 Biparental crosses being made at the Hawaiian Sugar Planters Experiment Station Four or five tassels each of the male and female varieties are placed under a lantern Note that the stalks have been placed in buckets Each bucket contains a weak sulphur dioxide solution which maintains the stalk and the arrow in a fresh condition

unconventional by the breeder unfamiliar with the work in sugarcane The hybridization procedures are facilitated by the technique of using detached arrows, as already described and by the utilization of male sterility or self incompatibility in some instances

(1) *Field Crosses* Field crosses, often used in the early days of sugarcane breeding, are made simply by collecting seed from open-pollinated tassels In this case only the female parent can be identified However, seed was usually collected only when two desired parents were growing in close proximity when this procedure was used

(2) *Biparental Crosses* Biparental crosses are crosses between two specific parents Arrows of the two parents may be brought together in isolated areas, or under lanterns (Fig 12 9), or hand pollination may be used If the female parent is self sterile, hybrid seed will be harvested If the female parent is self fertile, both selfed and crossed seeds will be obtained

(3) *Area Crosses* Area crosses may be made when several self sterile females are to be pollinated by the same male Cut or marcotted arrows of the females and one outstanding male are brought together in an isolated area This method is limited to use of male sterile or self incompatible females otherwise cross pollination between the females will occur also This procedure is more economical than biparental crosses, since several female parents may be pollinated in one crossing area by a common male parent

(4) *Melting Pot Crosses* Melting pot' crosses are made by bringing together arrows of a large number of varieties in an isolated area and permitting natural cross pollination to occur (Fig 12 10) Reshuffling of the arrows in the 'melting pot" will increase randomness and diversity of cross pollination Racks are generally built to support the tassels during the pollination period The "melting pot' is similar to the polycross' used in forage crop breeding Seed from melting pots are harvested and kept separate by clones, in which case the maternal parent will be known If clones are brought together which have been selected for some outstanding character, such as yield, sugar content, or red rot resistance, the seed harvested from the "melting pot" could be used for the first selection cycle in a recurrent selection procedure, or in a modified reciprocal recurrent selection programme [61]

B GROWING THE SEEDLINGS Sugarcane seed germinated in flats or beds soon after the se[ed] harvested (Figs 12 11 12 12) The seed bed usually covered after planting to prevent dry out Loss of seedlings from *Pythium* root rot or oth diseases within the seed bed may be reduced b sterilization, drenching beds regularly with a su able fungicide, and other sanitary measures Coimbatore, crossings are usually made in Octob or November and the beds planted in December January About 500 000 seedlings are grown ea year at Coimbatore

C FIELD NURSERIES The seedlings are trans planted to field nurseries when 6 to 12 weeks old Alternative procedures may be used Either th seedlings may be set out individually with spac of about 25 × 25 centimetres, or a group of 3 15 seedlings may be set in one bunch with spac of 25 centimetres between bunches in the ro 1 to 2 metres between rows (Fig 12 13 and 12

g 12 10 A melt ng pot or ol cross Selected var et es are rought together n an solated rea to perm t natural cross poll at on The tank at r ght conta n ulphur d ox de solut on wh ch s used to change b weekly the solu t on in the buckets n wh ch the detached stalks have been placed

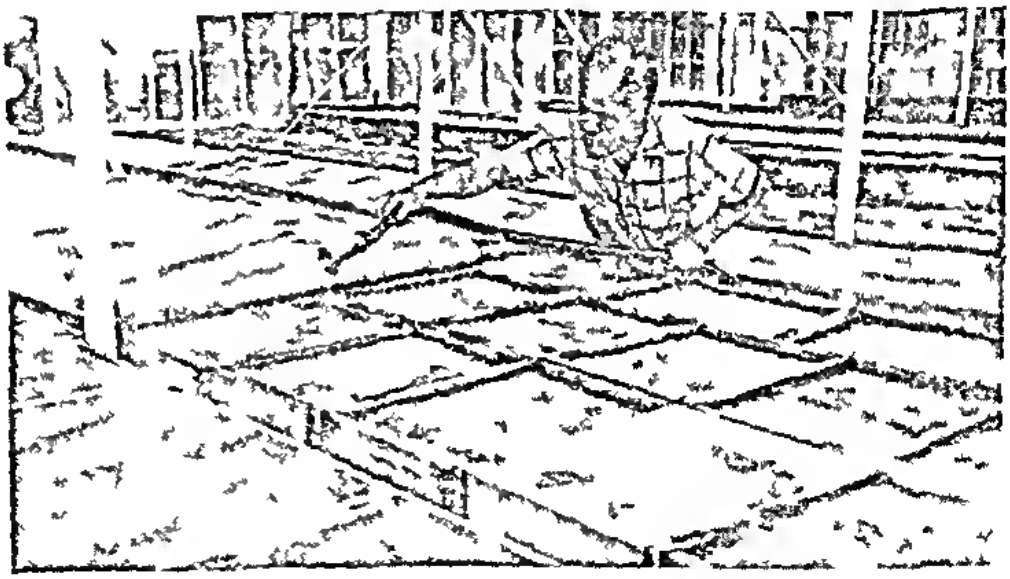

Fig 12 11 Water ng flats af er they have been planted w h sugarcane fuzz n the glasshouse at he Ha va an Sugar Plan ers Exper ment S at on Note the roll f wax paper at left wh ch s used co over the fla s un l the seeds c germ nate

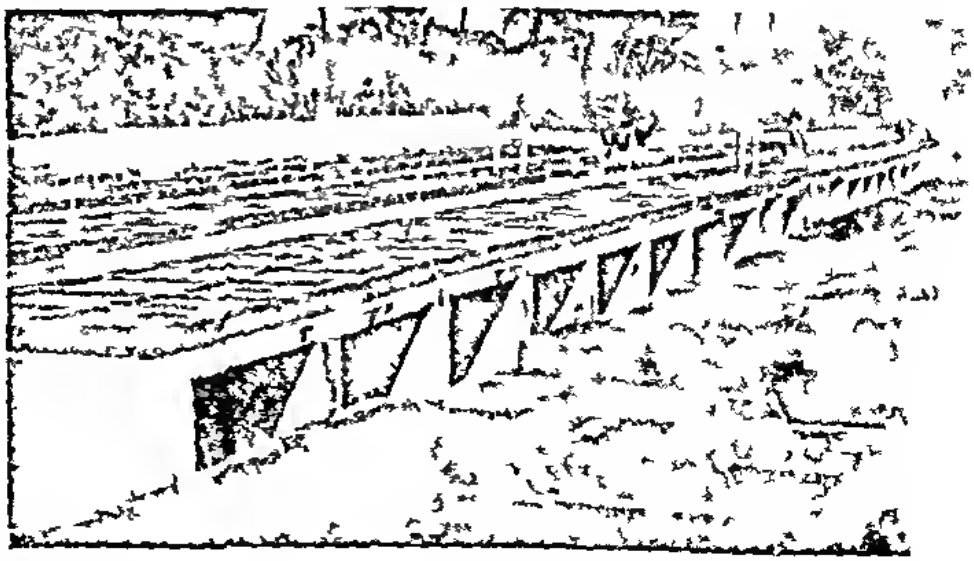

Fig 12 12 Sugarcane seedl ngs row ng n flats at Co mba ore hey are transplanted to field nurser es when 6 to 12 weeks old

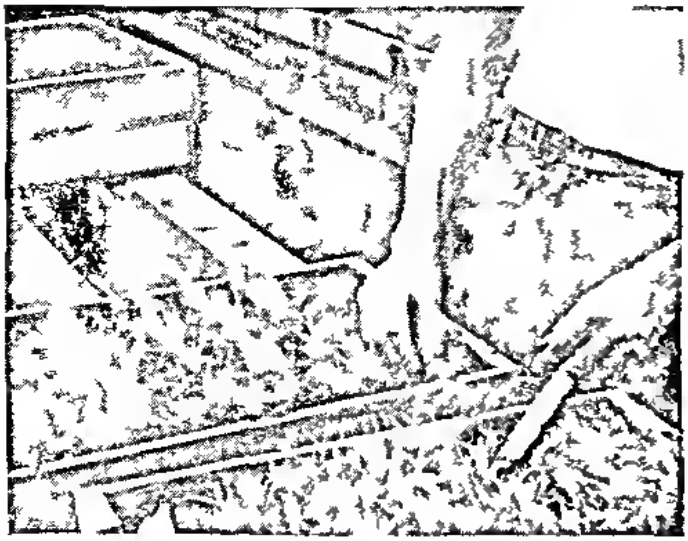

Fig 12 13 Transplanting bunches of sugarcane seedlings in the glasshouse Later the bunch of seedlings will be transplanted to the field

Fig 12 14 Bunch transplantation of seedlings to the field in Hawaii From 3 to 15 seedlings may be transplanted in a bunch to the field in rows 1 to 2 metres apart

Selected seedling plants from the space planted nursery may be transplanted to a second field nursery after four months where they will remain for another eight months but bunch plantings will usually remain uninterrupted for a full year (Fig 12 15) At Coimbatore about 400,000 seedlings are usually planted in the first ground nursery of which about 50,000 will be selected on the basis of vigour height tillering freedom from mosaic and other visible characteristics and transplanted to the second field nursery The bunch planting technique was developed in Hawaii and is practiced in areas where high labour cost or restricted land facilities limit the number of seedlings that can be handled by individual transplantation procedures It is more difficult to evaluate individual canes within a bunch than when they are individually spaced and some good canes may be lost as a result but since resources are never unlimited the loss may be compensated for by the larger number of seedlings that can be grown with available resources [33 64] In either method observations are made on characteristics such as vigour height and thickness of cane width of leaf freedom from disease and percent total sugar

D FIRST CLONAL NURSERY At the end of one year superior canes are selected from the field nursery to plant a preliminary clonal trial (Fig 12 15) Each of the selected canes will be planted in a row the length of the row being determined by the amount of seed canes or setts available Canes grown in bunches do not tiller as freely as canes which have been individually spaced hence fewer setts will be available to plant the clonal nursery from canes selected from bunch plantings as compared to canes grown in space plantings The first clonal nursery is grown for one year Appropriate check plots of standard varieties or clones are included for comparison Observations are made on vigour tillering height and thickness of cane flowering behaviour disease resistance sugar content and other characteristics At Coimbatore about 4 000 canes are selected from the field nurseries each year for planting the first clonal nursery If sufficient setts are available clones may be planted in a disease nursery in addition

E SECOND CLONAL NURSERY Clones with economically valuable characteristics such as high yield and sugar content or disease resistance will be selected after one year from the first clonal nursery to plant a second clonal nursery (Fig 12 15) The second nursery may be harvested for yields and will include appropriate commercial varieties for comparison The yield trial may be a single row of each clone or the clones may be replicated depending upon the amount of seed canes available Observations of yield disease resistance sugar content and quality, and other desirable characteristics

will be made At Coimbatore about 400 clones are selected from the first clonal nursery each year to plant the second clonal nursery

F MULTIPLICATION AND DISTRIBUTION OF CANES

Superior clones from the second clonal nursery are selected for multiplication and further testing At Coimbatore 10 to 15 of the superior canes are selected each year, given Co numbers, multiplied for one year, and then distributed as setts to the various state sugarcane research stations for testing Canes found adapted and superior after 3 to 5 years of further testing in the different states may then be released by the state research station for utilization in cultivators' fields

Sugarcane Breeding Institute, Coimbatore. The Sugarcane Breeding Institute was established in Coimbatore, India in 1912 [50] At the beginning work was concentrated on development of improved cane varieties for the northern subtropical regions where most of the sugarcane is grown in India Since 1926 breeding for the southern tropical regions has been in progress also The Sugarcane Breeding Institute was located at Coimbatore because sugarcane flowers and sets seed much more freely in that area than in the sugarcane production areas of north India Crosses are made at Coimbatore and selection of seedlings and preliminary testing of clones are carried out there before clones are sent to the states for testing In addition, crossed seeds or seedlings may be sent to the state sugarcane stations for evaluation and selection All clones sent out from Coimbatore are labelled by the letters Co and a number Substations of the Sugarcane Breeding Institute have been established at Karnal, Punjab, in the western subtropical region, and Cannanore, Kerala, on the peninsular west coast

Mutation Breeding. As in other crops irradiation or chemical mutagens may be used to induce mutations in sugarcane thereby increasing genetic variability [46] In seed propagated crops such as wheat or rice, seeds are irradiated and mutations arise within somatic cells of the seed embryo These give rise to bud or tiller mutations in the M_1 generation and mutant plants may be selected in the M_2 generation In sugarcane, which is a vegetatively propagated plant, nodal buds may be exposed to radiation fields and somatic mutations induced in addition to seed irradiation

Actually the genetic variability in sugarcane is already vast and the difficulties that would be encountered in recognizing variability, particularly mutants affecting quantitative characters, is very great Therefore, mutation breeding does not seem to offer advantages over conventional breeding procedures, unless it is possible to uncover useful mutants unavailable in present populations Following treatment of seeds in other crops with mutagens the M_1 plants are normally self pollinated in order that recessive mutant genes may be obtained in a homozygous condition in the M_1 This would be difficult to accomplish in sugarcane, and practically impossible in self sterile clones Somatic mutations, following radiation of nodal buds, usually give rise to mutant sectors or chimeras in which a nodal bud must be included if it is to be propagated Finding favourable mutants under these circumstances would be rather rare also [46]

Polyploidy. Since sugarcane is already a complex polyploid, possibility of economic improvement by further increase of chromosome number by autoploidy does not appear to offer much opportunity Polyploidy may be useful in consummating interspecific crosses with low chromosome number species of related genera

BREEDING OBJECTIVES

The principal objectives in breeding sugarcane are yield, adaptation to frost, drought and other environmental adversities, disease resistance, insect resistance, and sugar content and quality Yield and sugar content have been given major importanec in the past although disease resistance has been important in some areas

Yield. The height, thickness of stalk, and tillering ability of the clone all contribute to the tonnage of cane harvested per hectare Hence, primary selection is always for vigour of growth and for tall, large barrelled canes with high tillering capacity Juiciness of the stem, and sugar content and recovery, are also important factors in the yield of sugar per hectare The canes of the wild *spontaneum* species are slender and pithy with practically no recovery of sugar, while canes of *S officinarum* are high in sugar More progress has been made in increasing total sugar yield by breeding for increased tonnage than has been made by breeding for increased sucrose content [35] Yield of cane harvested is also influenced by response to fertilization, [18] resistance to climatic adversities, and resistance to disease and insect pests, so these factors must also

be given consideration by the breeder Selection and testing should be done at high levels of fertilization and optimum levels of soil moisture since production needs in countries like India cannot be met without both superior varieties and advanced cultural practices which include maximum utilization of fertilization and irrigation facilities Improved varieties should stand without lodging, respond favourably to these cultural conditions, and produce high yields of cane and sugar

Lodging Resistance. Successful production of sugarcane at high fertility and optimum moisture levels requires that the sugarcane plant stand without lodging Lodged canes in many areas fail to develop full normal growth, provide favourable environments for the development of disease, and deteriorate in sugar content and quality Lodging resistance is dependent upon strong vigorous canes, a healthy and well developed root system, and freedom from disease or insect injury that will weaken the stalk and make it susceptible to lodging in wind or rain storms Height also is a consideration in lodging resistance While tall plants are necessary and desirable for maintaining high yield, they are more susceptible to damage by storms, and a balance between excessive height and reduced yield from shorter plants may need to be achieved Some selections of *S spontaneum* have strong root development which may be incorporated into commercial hybrids to enhance lodging resistance

Resistance to Frost, Drought, and Water logging. Resistance to cold and occasional frost is required for sugarcane varieties in north India The indigenous varieties of north India *S barberi* and *S sinense*, have tolerance to these unfavourable conditions and to drought, as also do the wild canes of *S spontaneum* Combining the hardiness of the indigenous canes of north India with the high sugar content and yield of *S officinarum* has been a major objective in the breeding of sugarcane for India. It has been observed that certain clones of *S spontaneum* are able to withstand waterlogged conditions for long periods Such clones might be useful as parent materials in breeding commercial types which would grow more productively on waterlogged soils than present varieties The tolerance to waterlogging is characterized by the production of a large matrix of fibrous roots extending from the base of the stem to the surface of the water [56]

Disease Resistance. The breeding of sugarcane has been closely related to the outbreaks of serious diseases in the crop The sereh disease, presumed to be caused by a virus, forced the abandonment of the Black Cheribon variety of the noble sugarcanes in Java Another virus disease, mosaic, combined with red rot, almost forced abandonment of the sugarcane industry in Louisiana The disease was later controlled by breeding resistant varieties Fiji disease caused serious damage to sugarcane in the islands of that name until brought under control by breeding Variety decline, widely experienced and the reason for frequent variety shifts, is believed mainly to result from changes in pathogens such as *Pythium*, red rot, and others

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A RED ROT Red rot is caused by the fungus *Collectotrichum falcatum* Red rot infection may lead to poor germination of setts, rotting of the root system, and rotting and breakdown of the stalk [2,26,36] Losses in yield of cane and sugar may be high when red rot is present Damage is generally more severe in subtropical areas such as north India than in the tropical climates where germination and growth of setts is more rapid The fungus may invade any part of the plant but frequently enters through borer injuries and leaf sheath scars Infection may remain unnoticed until the interior of the stalk has become badly degenerated Lesions on leaves or wounds on stalks are usually dark or blood red in

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Fig 12 16 Drawing a sample of juice from a sugarcane stalk and reading the Brix with a hand refractometer This procedure gives the sugarcane breeder a simple and direct means of estimating sucrose content of small samples of juice [35]

colour and easily identified Planting resistant varieties is the primary method for control and *S spontaneum* has been the chief source of resistance *S officinarum* and *S barberi* are susceptible Inoculation of seedling plants at the age of 7 to 8 months may be made by puncturing the stem and introducing a mixture of virulent strains or by breaking off the lower green leaves and spraying the wound with inoculum of the red rot organism There are numerous physiologic strains of the red rot organism [55]

B SMUT The smut fungus *Ustilago scitaminea* Syd infects the plant by wind blown spores which fall on the bud or through the setts after they are planted in the ground Infected plants are stunted and produce a whiplike shoot at the growing point Varieties of *S barberi* and *S spontaneum* are largely susceptible but *S officinarum* varieties are resistant [38]

C MOSAIC Mosaic one of the most widely distributed sugarcane diseases is caused by a virus which produces mottling of the leaf, and in severe cases stunting and loss of yield [26,36] Many strains of the virus which are transmitted by aphids or in seed canes have been identified [60] Mosaic causes most damage in the subtropics where conditions for production of sugarcane are less favourable than in the tropics The severity of the mosaic on the growth of the plant varies with the variety of sugarcane and the strain of the virus Artificial inoculations are made with juice from an infected plant *S spontaneum* is largely resistant while *S officinarum* and *S barberi* are susceptible

D RATOON STUNTING Ratoon stunting is also caused by a virus It may be transmitted by planting diseased seed canes or by juice of the diseased plant carried on tools or cutting knives [26,36] Infected plants are retarded in growth and ratoons are stunted Setts from stunted ratoons produce stunted plants. Varieties vary in resistance but none are immune Little information is available on resistance in India.

E RUST In India rust is caused by *Puccinia erianthi* of which six races have been identified [54] One cane Co 475 was abandoned due to susceptibility to rust Resistance is present both in *S officinarum* and *S robustum*

F ROOT ROT Root rots may be caused by many organisms but it is generally believed that the

Pythium root rot, *Pythium arrhenomanes*, is a major contributor to the malady known as variety decline The species is extremely variable and many races of this organism occur Destruction of roots, severe wilting, stunting, and yellowing of leaves are symptoms Losses have been reduced by breeding resistant varieties, but some symptoms may be observed even on the more resistant hybrids Resistance is found in forms of *S barberi*, *S sinense* and *S spontaneum* while *S officinarum* is susceptible

Insect Resistance. The worst insect pests attacking sugarcane in India are the borers of which the top shoot borer (*Scirpophaga nivella* F), early shoot borer (*Chilotraea infuscatellus* Snell), and the internode borer (*Proceras indicus* Kapur) are the most common Differences in resistance of clones to the borers have been observed at Coimbatore Resistance may result from unattractiveness of the leaf for egg deposition, inability of young borers to become established, high fibre which hinders feeding of borers, or tolerance and ability to produce good yields in spite of borer attack

Quality. Various factors may be considered in quality of sugarcane but in general we may include millability, sugar content of juice, and quality of juice Millability refers to characteristics of the cane that makes it possible to recover the sucrose from the stalk by normal methods of extraction Characteristics desirable for good millability are moderate hardness of rind, good length of fibre, long internodes, and low fibre-sucrose ratio These affect the power required to extract the juice and the possible loss of sugar in the bagasse Sugar content of juice is important as it, along with yield of juice, determines the sugar yield per hectare The most important factor in quality of the juice is the percent sucrose, but other factors of importance are total solids, brix (Fig 12 16), and the non-sugar fraction of the juice Little progress has been made in increasing sucrose content in hybrid canes over the content of the best of the older clones of *S officinarum*.[35]

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13

Breeding Potato

Potato is one of the most productive and widely grown food crops It is cultivated both in large tracts and in home gardens and provides a cheap and nutritious food The potato is unique and different from other crops discussed in this textbook in that the food materials are stored in underground parts, called tubers (Fig 13 1) Tuberization is not favoured by high temperatures, and this constitutes one of the handicaps to growing potato in the tropical or subtropical areas of south and southeast Asia High temperatures also create problems in storage and seed maintenance of potato which further limits the production and utilization of potato in the warmer climates of the world In India, potato growing has been concentrated in the hill areas where a more temperate climate is found, or potato is grown in the autumn and winter months when cooler temperatures prevail

Breeding of potatoes is also unique compared to other crops discussed in this textbook, except for sugarcane, since the potato is a vegetatively propagated plant It flowers sparingly, and then only in certain favourable climates, and it has a high degree of sterility Since flowering and seed production are requirements for obtaining genetic recombinations, the shy flowering and seed setting in the potato are severe handicaps to the breeder In one way, however, vegetative propagation has a distinct advantage to the breeder since superior genetic strains, once they are identified, may be increased and maintained by clonal propagation, using tubers, just as the sugarcane breeder maintains and propagates superior clones of sugarcane using seedcanes or setts

The common cultivated potato is indigenous to the Central Andean region of South America It was carried to Europe by the early Spanish explorers in the sixteenth century From Europe it was introduced into India, the United States, and other areas of the world [40 56 63]

CLASSIFICATION

The potato belongs to the genus *Solanum*, in the family *Solonaceae*, or nightshade family This family

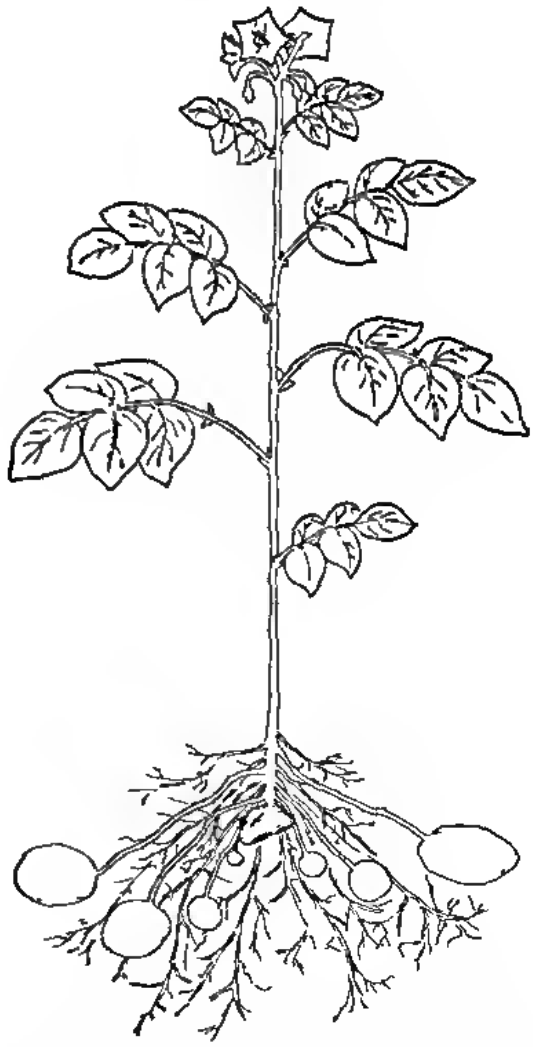


Fig 13 1 Plant of potato showing reproduction by flowers and tubers In the potato plant the food materials are stored in underground parts called tubers

also includes many other important commercial plants such as tomato, tobacco, egg plant, capsicum pepper, and petunia, as well as poisonous nightshades The genus *Solanum* contains about 2,000 species, including over 100 tuber-bearing species Most of the species of *Solanum* are herbs or small thorny shrubs A comprehensive classification of the potato and its wild relatives has recently been made by Correll[4] and a revised classification of the tuber bearing species has been published by Hawkes [13] As might be expected with such a vast and diverse group of species, schemes of classification vary in details according to the views of the different workers Also, very little is known about the genetic and evolutionary relationships of the various species, information which would be useful to the taxonomist in developing a classification

The commercial cultivated potato belongs to the species *Solanum tuberosum* This is the only species of the tuber bearing *Solanums* that has been cultivated outside its native area *Solanum tuberosum* is generally believed to have originated in the Andes region of South Peru and Bolivia [14 47] From there, the potato reached Europe, and, after prolonged selection for tuber yield and earlier maturity under longer day lengths than prevailed in its native home, further alterations in plant and leaf characteristics and in photoperiodic response have taken place Types with similar plant and leaf characteristics and photoperiodic response are found growing also in the long day conditions of Chile This led early Russian investigators to suggest that the European potato came from Chile, but this view has generally been refuted in recent years [47] It is now considered more likely that Chile may be a secondary centre of origin of *Solanum tuberosum*, where evolutionary changes occurred similar to those which later took place under selection in Europe Further evidence for the Andean region of Peru as the original home of the common cultivated potato is the fact that the native cultivated diploid species, *S stenotomum*, believed to be a progenitor of the tetraploid *tuberosum* species, is also found growing in that area [11]

Species of wild potato are also found in Mexico, southwestern U S A , Guatemala and other countries in Central America This area is considered to be, along with the Central Andean region of Peru Bolivia, a primary centre of origin for the potato It has been postulated that the tuber-bearing species may have originated in the Mexican area and migrated southward into the Andes in very early times, where they hybridized with native Andean species

VARIETIES

Variety in the potato refers to the vegetative increase, normally by tubers, from a single plant As in sugarcane, which is also vegetatively propagated, variety refers to a clone We have already referred to the early introduction of the potato into Europe and subsequently into India and other areas of the world Potato first reached India in the early part of the 17th century, probably by Portuguese traders who brought it from Europe

Many desi, or local, and introduced varieties have been grown in India and other countries of south and southeast Asia The introductions were largely European varieties After a variety is introduced and grown in a locality for some time it often acquires a local name Also, unrelated varieties are often grown under the same name, as well as the same variety being grown under several names In a survey of commercial potatoes collected from the different states in India and a few other countries, such as Afghanistan, Burma, Nepal, and Pakistan, only 16 distinct desi varieties could be recognized [40] These represented indigenous types which had been introduced a long time ago and have now lost identity regarding their origin Some are similar to original European varieties [54] Among the 16 varieties Darjeeling Red Round, Phulwa, Gola, and Sathoo are perhaps the best known The variety Darjeeling Red Round was found growing under 49 different names

Sixteen European introductions are listed, according to the same survey, as established commercial varieties in India [40] The most important of these are Up to Date, Magnum Bonum Great Scot, Ben Cruachan, and President The desi and European varieties are now being replaced by varieties developed in India such as Kufri Kisan, Kufri Kuber, Kufri Kundan, and Kufri Sindhuri All of these varieties were developed in the Potato Research Institute, Simla These and many other varieties are described in Pushkarnath's "Potato in India, Varieties "[40] Histories and descriptions of the European varieties have been prepared by Salaman [48]

CYTOLOGY AND GENETICS OF POTATO

Many studies have been made of the cytology and genetics of potato [16 18 23 58 59] Among other problems, consideration has been given to the cytological relationships between the tuber bearing species of *Solanum* The basic chromosome number of this group of species is generally considered to be 12 A basic number of 6 has also been suggested If the latter is correct then an unknown wild species with a chromosome number of 6 must have been a progenitor of the present species since no species with the chromosome number of $n = 6$ is known today There are five levels of polyploidy in the tuber bearing *Solanum,* with somatic chromosome numbers of $2n = 24$, $2n = 36$, $2n = 48$, $2n = 60$, and $2n = 72$ The commercially cultivated species, *Solanum tuberosum* is a tetraploid with the chromosome number $2n = 48$

Solanum tuberosum was first considered to be an autotetraploid, however, more recent views hold that it is more probably a segmental alloploid, derived possibly from crosses between the cultivated diploid species, *S stenotomum,* and the wild diploid species *S sparsipilum* [11 12] Cytological studies in the potato have been difficult owing to the small size of the chromosomes the absence of distinct genome differentiation, the accumulation of chromosomal structural changes, and meiotic irregularities in vegetatively propagated clones

Attempts have been made to establish genomic relationships between the tuber bearing species of *Solanum*[13 23] but these have not progressed very far Many species differ from each other by very small chromosome segments which do not affect pairing in species hybrids but which result in sterile F_1 plants or weak and unthrifty F_2 progenies [12] Tentatively, two series of genomes have been identified, an *A* series (A_1, A_2, A_3, A_4) of South American origin and a *B* series (B_1, B_2 B_3, B_4) of Mexican origin [14]

The genetics of the potato has been reviewed by Swaminathan and Howard[53] and Howard [16] Inheritance studies have been made of numerous important economic characteristics including disease resistance Genetic studies in the potato are difficult owing to the heterozygous nature of the clonally propagated varieties, the shy flowering and sterility in potato, the segregation and loss of vigour after selfing, and the occasional occurrence of bud mutations or chimeras [59] The inheritance of some specific economic characteristics will be discussed along with the objectives of breeding potato

Induced polyploids may be produced in potato by treating seeds with a weak colchicine solution or by treating a clone Doubling the chromosome number of the clone is more difficult but some success has been attained by placing a colchicine solution in leaf axils of decapitated shoots, or by covering the eyes of the potato with lanolin paste containing colchicine

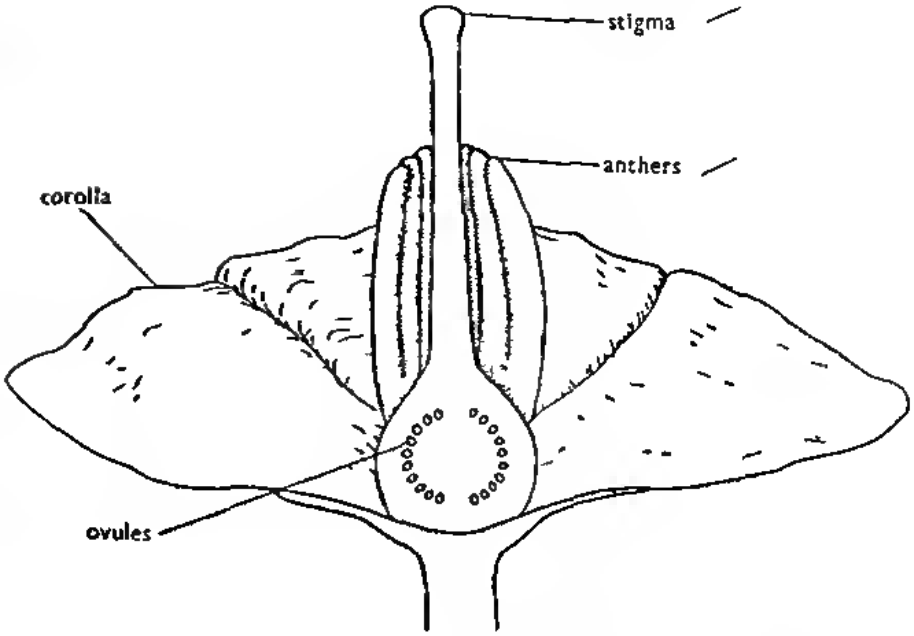
Haploid plants of potato may be useful in genetic and breeding studies By successively obtaining haploids and then doubling the chromsome number of the haploids, the possibility of obtaining genetically homozygous clones at a rate comparable to selfing in diploids is provided [15] Such clones would be different from normal clones which are highly heterozygous The haploid plants occur occasionally when the tetraploid species, *S tuberosum,* is pollinated by pollen from a diploid species If the diploid has a dominant genetic marker, such as purple pigmentation, the haploid seedlings may be easily recognized since they will lack the pigmentation

BOTANY OF POTATO

The potato flower contains five sepals, petals, and a two celled ovary with a single style and bilobed stigma The corolla varies in size with the variety The colour of the corolla varies from purplish to nearly white and is a distinguishing varietal character The petals are united and tubular The stamens are attached to the corolla tube and bear erect anthers which form a close column or cone around the style (Fig 13 2) In some clones, mature flowers are never formed as the buds dehisce Pollen production in most commercial varieties is very poor, many varieties produce practically no pollen at all [41] Seeds are produced in a berry, often called the 'seed ball" or "apple' (Fig 13 3A) The seed balls fail to form in many commercial varieties due to failure to obtain pollination or fertilization While potato species and varieties vary in the abundance of flowers produced, most varieties of the cultivated species are moderate to poor in flowering and few bear flowers very profusely [37]

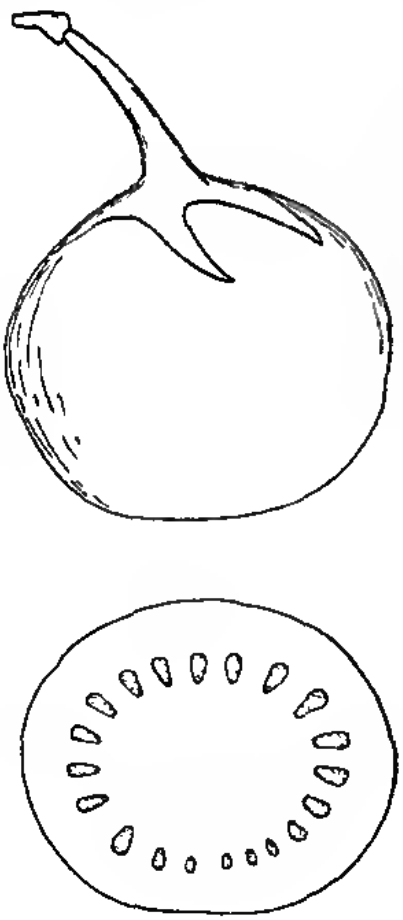
Flowers in the cultivated potato open mostly in early morning, although a few may continue to open throughout the day Self pollination is the rule and cross pollination by wind or insects occurs

13 2A



13 2B

Fig 13 2 A Flower of potato Note how anthers form a close column or cone around the style B Longitudinal section of a potato flower showing (*a*) corolla, (*b*) anthers (*c*) style and stigma protruding above the cone of anthers and (*d*) berry or seed ball



13 3A

13 3B

Fig 13 3 Reproductive structures in potato A Sexual reproduction by berries or "seed balls' B Asexual reproduction by tubers The sprout has germinated from the bud in the eye of the tuber

infrequently [37 41] Germination of the pollen is completed after 30 minutes and the ovary is fertilized within 12 hours [41] Viable pollen is long lived and may be dessicated and stored at low temperatures for as much as a year Obstacles to seed production in the potato include (*a*) failure to flower, (*b*) dropping of buds and flowers either before or after fertilization, (*c*) low pollen production and failure to produce viable pollen, (*d*) male sterility, and (*e*) self incompatibility

Asexual reproduction in the potato is by tubers The sprouts arise by germination of buds in the eye of the tuber (Fig 13 3B) The tuber varies in the period of dormancy according to the variety, but in general the dormant period is relatively short Vegetative reproduction is also possible by rooting stem cuttings

Non Flowering in Potato. Sparse or shy flowering in potato may be inherent but it is also affected by the environment Breeding and selection for high tuber production has resulted in the development of many varieties which flower only rarely This has been no handicap in commercial potato production since the potato is propagated by tubers and maintenance of strains is not dependent upon seed production In fact, seedlings which form berries profusely generally are poor yielders so they are seldom increased by breeders But, as already pointed out, shy flowering is a handicap to the breeder Flowering in potato is also influenced by climate In India, the potato flowers most profusely during summer in the hills of northern India The climatic factors favouring flowering there are long summer days abundant rainfall, high humidity, and cool temperatures Potato flowers very poorly when grown as a winter crop in the plains This has led to the location of the Potato Research Institute at Simla, in the northern hills of India, since flowering and seed production are essential for genetic improvement of the potato by recombination breeding Various techniques are often used to induce flowering such as periodic removal of tubers, girdling or constriction of the stem, and grafting of young potato shoots onto tomato or other compatible *Solanaceous* plants [26]

Sterility and Incompatibility Poor seed set in flowers of the cultivated potato may result from male sterility or incompatibility In the cultivated varieties of *S tuberosum* failure to produce pollen, or production of poor quality pollen, is a common cause of sterility In India, of 247 varieties examined 70 percent were found to be male sterile, producing no pollen or only a few sterile grains [36 42] The failure to produce pollen may be an inherent characteristic with sterility dominant to fertility [36 48] Presence of a tetrasomic gene, which is lethal when present in a homozygous condition, or partly lethal when present in the heterozygous condition, has also been reported [24]

Incompatibility is present in different species of the genus *Solanum* In a study of several diploid species, it has been shown that incompatibility is genetically controlled by a series of alleles, S_1, S_2 S_3 and so on [32 33 34] In one diploid species, the incompatibility system is modified by a factor, *R* which when present in the style prevents fertilization from a pollen tube carrying *S* alleles [35]

Crossing Techniques. Emasculation is done in the evening Flower buds that will open the next morning are selected and the rest of the buds and flowers in the bunch are removed The flower buds standing above the leaves are better for the purpose as they generally have more fully developed floral stalks The petals of the selected flowers are gently pushed apart along the sutures and the five stamens removed with fine pointed forceps [46] The emasculated flowers are then bagged In places like Simla, where crossing is done in the rainy season use of thick butter paper bags and supports to prevent the bag from falling over have been found to be advantageous [37] Inserting a branch with one or two leaves into the bag helps in maintaining a humid climate inside the bag In fully self sterile lines emasculation is unnecessary

Pollination is done in the early morning [37 46 56] Fully mature anthers, from varieties known to possess viable pollen, are selected and placed in a petri dish or other small container Pollen is collected from the anther on a pen knife or a pair of forceps and spread over the stigma The anther may also be held in the hand in an inverted position and the pollen released over the stigma by splitting open the anther lobe with small fine pointed forceps After pollination the flowers are again bagged Setting of seed may be observed in about 7 to 10 days The bags may be left on until the berries are mature Since few varieties produce viable pollen, seed setting is usually poor

Crossing in the field is difficult during the rainy season, yet in India the best flowering of potato is

obtained with potato growing in the hills during the monsoon period To obviate this difficulty in crossing, cut floral branches from the fields are often grown in the glasshouse [22] In this procedure the floral branches are collected and taken into the glasshouse The stems are cut under water and placed in a sterile solution of 5 p p m indole butyric acid for 24 hours and then transferred to wide mouth bottles containing 1 1000 Shive's nutrient solution Streptomycin sulphate is added to the nutrient solution to control soft rot infection The nutrient solution is replaced with fresh solu tions every fifteen days Spraying the plants with 40 p p m giberellic acid 24 hours before collecting the floral branches helps to prevent dropping of buds and open flowers Satisfactory pollinations can be made on the cut branches and the branches will remain alive until the berries are developed Seed setting on cut branches in the glasshouse is higher than that obtained in the field at Simla, particularly in varieties like Great Scot where abscission of the buds and flowers is common

Interspecific Hybridization. The large number and variability of species of *Solanum* provides the plant breeder with a huge supply of germ plasms from which to obtain genetic diversity, providing of course that the useful genes from the other species can be transferred to the cultivated species Information regarding the crossability of species between the various polyploid series is still rather fragmentary In general the diploid species cross more readily with the tetraploid species than among themselves Some interspecific crosses can be made in one direction only, reciprocal crosses being sterile For example, *S demissum* (6*n*), used as a source of blight resistance, can be crossed with *S tuberosum* (4*n*) only when used as a female parent [5] Failure to produce seeds following interspecific crosses in the tuber-bearing *Solanums* may be due to (*a*) inhibition of pollen tubes in the style, (*b*) failure of the ovary to develop following fertiliza tion, or (*c*) abortion of embryos following fertiliza tion To overcome the difficulties encountered in interspecific hybridization several techniques have been adopted [36] These may be summarized as follows

(*1*) Doubling the chromosome number of the diploid species and making the cross at the tetraploid level

(*2*) Making an amphidiploid by crossing two diploid species and crossing at the tetraploid level

(*3*) Doubling the chromosome number of a tetraploid species and crossing the autopolyploid with a tetraploid

(*4*) Crossing the cultivated type with a wild type and backcrossing to the cultivated type until the wild genes are eliminated except for dominant genes for the desirable character being selected

Pollen-stigma incompatibility may sometimes be overcome by (*a*) pollination in bud stage, (*b*) low temperature during period of pollen tube growth, (*c*) removal of stigma and a portion of the style and applying pollen in an agar-sucrose gelatin solution to the cut surface [57]

METHODS OF BREEDING POTATO

Potato varieties have been developed by introduction, selection, and hybridization Irradiation has also been used in attempts to increase genetic variability in desirable traits, and polyploidy has been used as an aid to interspecific hybridization

Introduction and Germ Plasm Collections. Many varieties of potato have been introduced into India and other countries of south and southeast Asia, since the early 17th century Since seed stocks degenerated very quickly in India, new introductions of old varieties as well as new varieties were made periodically At present more than 1500 commercial types and 120 wild species of *Solanum* are being maintained at the Central Potato Research Institute at Simla This collection represents local varieties as well as exotic types collected from all over the world In the recent publication, 'Potato in India, Varieties,' [49] about 350 exotic varieties are described, but of these only about 16 are now important commercially in India Varieties like Magnum Bonum, Craigs Defiance, and Up to Date are good examples of introduced varieties currently grown in India for commercial cultivation The variety, Magnum Bonum raised by Mr J Clark of England, was first introduced into India in 1892 Because of its good yielding potentialities and tuber quality, it has been extensively grown in India Similarly, the variety Craigs Defiance was introduced into India from Scotland in 1936 and later became popular in several regions of the country The variety Up to Date was first introduced into India from England in 1906, however, the present seed stock of the Up to-Date variety was increased from an introduction of a disease-free clone selected

from a grower's field in northern Ireland in 1946 [40] In addition to being grown directly, introductions are used in hybridization programmes to combine desirable qualities of the introduced variety with those of a desi variety or another introduction Hybrid O N 45 was developed at the Central Potato Research Institute, Simla from a cross involving Katahdin, an introduction from the U S A , and President, an introduction from the Netherlands Similarly, the variety Kufri Kisan released in the year 1953 for the plains area, is a complex cross involving Ekishirazu, a Japanese variety, Katahdin, an American variety, Phulwa, a desi variety, and Up to Date a Scottish variety Detailed descriptions of varieties introduced into India will be found in "Potato in India, Varieties' [40]

For many years, breeding in Europe, Asia and elsewhere was based largely on a few early introductions from the Americas Little consideration was given to building up germ plasm collections of related wild and cultivated species or utilizing these exotic materials in breeding programmes In 1925, a Russian expedition was sent to the Andean region of South America to collect potato in its native home The expedition called attention to the vast diversity of species of *Solanum* which might have breeding value Since then many expeditions have been made into South and Central America and Mexico and large collections of *Solanum* species are now maintained in Great Britain, Netherlands, U S A Russia, Peru, Columbia, and other countries These collections are providing the breeders with sources of genes for disease resistance, frost resistance, insect resistance and other characters [29 65]

Clonal Section. The desi or local varieties of India, like Darjeeling Red Round, Phulwa, Chamba Red, and others were introduced into India many years ago but during the course of time their original history has been lost These varieties as they exist today in different areas of India have been subjected to natural selection as well as artificial selection by the growers Since an improved variety is a single clone, clonal selection within varieties is not generally a fruitful procedure in breeding However, in older varieties genetic variation, probably resulting from occurrence of mutations or chimeras, or segregation from chance seedlings, may be present Selection from heterozygous desi types such as those listed above sometimes leads to the isolation of desirable or superior clones Darjeeling Red Round is a local variety which shows wide clonal variation in characters The variety, Kufri Red, was developed from a disease free clone selected from Darjeeling Red Round It was released as a variety in 1957 Since potato is a vegetatively propagated crop, a clonal selection isolated from a genetically mixed population can be readily maintained A single tuber, or the tubers from a single plant, is the unit for selection with the clonal selection procedure Frequently the gains obtained through clonal selection come from obtaining a virus free stock

Hybridization. Hybridization has been the principal method of improving the potato in recent years Intervarietal crosses are made between commercial varieties to bring together the desirable characters of the varieties into one hybrid The hybrid variety, Kufri Kundan, was developed at the Central Potato Research Institute, Simla, from a cross between Ekishirazu and Katahdin, introductions from Japan and U S A , respectively The crosses may be simple involving only two varieties or may be multiple involving several varieties Kufri Kisan was developed from a succession of three crosses involving three introductions and a desi variety

Since potato is a vegetatively propagated crop, commercial varieties are heterozygous and segregation of characters will be found in the F_1 generation following hybridization Clonal selection is therefore practiced in the F_1 generation and rarely is an F_2 generation grown

In India, selection following hybridization was formerly carried out at Simla where the crosses were made At Simla, potato is grown only under long day conditions of summer In the plains, potato is grown commercially in short day conditions of autumn or winter It has been found difficult to select and develop varieties at Simla under long day conditions with proper adaptability and desirable maturity for production in the short day conditions in the plains or in other agronomic regions of the country which differ from the Simla area in photoperiod, disease, and other environmental respects For this reason the breeding scheme has been altered recently (Fig 13 4) The crosses are now made at Simla and the F_1 seeds are sent to the Regional Station in the plains at Jullundur, Punjab where they are grown and selections made during the short days of autumn At Jullundur,

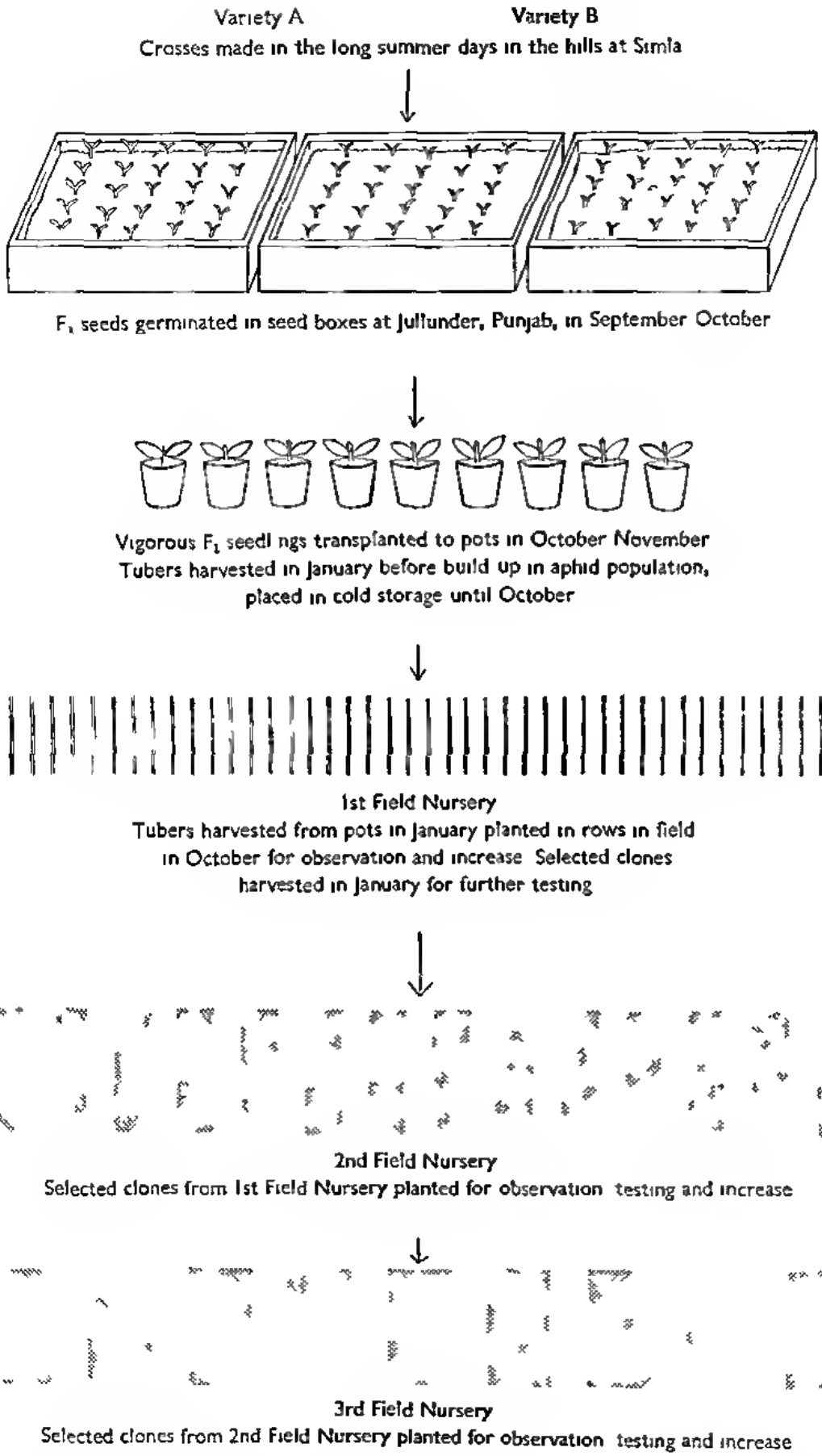
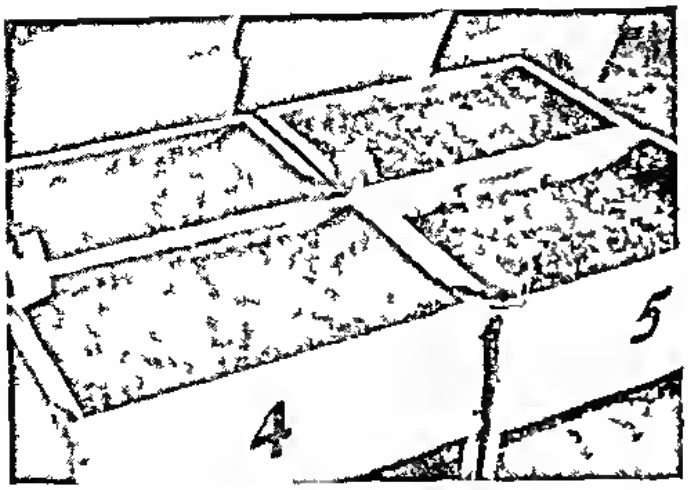


Fig 13 4 Scheme for growing F_1 potato plants following hybridization and for screening and testing the clones



13 5A

13 5B

13 5C

13 5D

F g 13 5 Growing F_1 potato plants and test ng clones A F potato seedl ngs n flats B Potato seedl ngs after transplan at on nto pots C 1st potato field nursery Jullundur Clones are planted n rows about 1 metre in length D 2nd potato field nursery Jullundur Clones are planted n ro s about 2 to 3 metres in length

the seeds are first sown in wooden boxes (Fig 13 5A) and later transplanted to earthen pots (Fig 13 5B) and grown to maturity during a period in autumn when aphid populations are low to minimize the possibility of obtaining virus infections The tubers obtained from each plant are then grown in individual F_1 rows during the next season (Fig 13 5C) Each row represents the clonal increase from a single F_1 plant The next season the clones will be grown in longer rows and replicated if sufficient seed tubers are available (Fig 13 5D) Selected clones after seed tubers have been increased in sufficient quantity are then sent to the different regional state research stations in the hills and plains, for further selection, screening and testing to find those varieties suited to the respective re g ons This procedure permits observat on selec tion and testing of the strains to be carried out under the short day conditions of the plains or in the agroclimatic region where the variety is to be grown In the plains at Jullundur increase and testing of varieties and strains is carried out in autumn which is a period with a low aphid popula tion This is necessary to reduce the infestation of stocks of seed tubers with virus diseases transmitted by the aphids Crossing is not done in the fields in the plains because (*a*) only short day varieties flower in the plains thus limiting the cho ce of the parent variety (*b*) the parent varieties may not flower at the same time (*c*) fertility is reduced and

some varieties do not set berries in short days, and (*d*) the risk of frost injury to the breeding materials reduces the chance for success

A large number of interspecific crosses have been attempted in potato Interspecific crosses often involve special techniques in order to ensure fertility and seed set A few of the techniques that may be used have been discussed earlier Only limited success has been attained with interspecific hybridization [27] Interspecific crosses are usually made to transfer a specific desirable trait present in the wild species The variety Kufri Kuber, released in 1958, was developed from the cross (*Solanum curtilobum* × *S tuberosum*) × *S andigena* [40] *S curtilobum* is a pentaploid ($2n = 60$), the other species are tetraploids ($2n = 48$) The new variety has a low rate of degeneration in the plains as compared to Up to Date Interspecific crosses have been used in the breeding of varieties for disease resistance *S demissum* has been widely used in Europe and elsewhere as a source of resistance to the late blight disease

Inbreeding in potato may be used to fix particular characteristics in a variety before the variety is utilized in a breeding programme Because of the polyploid nature of the species and the quantitative nature of many of the characters studied, genetic variability has been reported to be high through the S_2 generation [52] Pollen fertility is reduced more in some varieties by inbreeding than in others

Use of Polyploidy. Since the commercial cultivated potato, *S tuberosum*, is tetraploid in nature, there is little chance that further induction of polyploidy alone will result in improvement of the crop However, induction of polyploidy has been successfully exploited in a number of cases to assist in making crosses between species differing in level of ploidy which otherwise would have been unsuccessful [36] Some of the procedures used in interspecific crosses have already been listed

Irradiation Breeding. Irradiation breeding may be utilized as a tool in bringing about changes in genes for particular characters and for increasing the range of genetic variability in a particular background In crops like potato which are asexually propagated, somatic mutations may be useful since the mutant plant may be increased as a clone X-ray and gamma radiation of tubers have been found to increase the keeping quality of the tubers by lengthening the dormancy period [21 53]

Central Potato Research Institute, Simla. The focus of the breeding work on potato in India is the Central Potato Research Institute, Simla [49 50 51] In addition to the headquarters at Simla and a research station in Patna, Bihar, there are five experimental and trial centres through India, two seed multiplication stations in the hills, and one potato wart testing station on wart infested soil near Darjeeling The first work at Simla was started in 1935 This station was located in the hills of north India because the long day, monsoon climate in the Simla area provides favourable conditions for potatoes to flower Due to the high altitude, it is also a relatively aphid free area and breeding stocks can be grown with a minimum of danger of virus infection It is the policy of the Institute to test new strains in their regional stations and also to make selections from their breeding plots available to the states where the strains may be tested for adaptation and possible increase as new varieties Varieties developed by this cooperative programme will be released jointly upon recommendation by the State and the Institute Varieties developed by the Central Potato Research Institute are given a name consisting of two words, the first word being Kufri Examples are Kufri Red, Kufri Kundan, and Kufri Sindhuri

OBJECTIVES IN BREEDING POTATO

The objectives in a breeding programme must be clearly defined if the breeder is to be successful in obtaining the desired improvements in a variety Selection of parents will depend on the objectives in mind Furthermore, the objectives should be such that, besides increasing yield, they will lead to the improvement in other characters that will increase the usefulness of the variety to the cultivator The main objectives of breeding potato in India are high yield, regional adaptability, heat, frost, and drought resistance, disease resistance, insect resistance, and quality [38] Each will be discussed briefly

Breeding for High Yield. The important overall objective in breeding potato is high yield of tubers At Simla and the trial centres, many commercial varieties have been evaluated for their yielding ability and crosses made between suitable varieties in attempts to find hybrid combinations that will be better yielding varieties An example is the variety Kufri Sindhuri, selected from a cross between

Kufri Red and Kufri Kundan, which has yielded well above either of the parent varieties Yield is, however, related to other plant characteristics, such as adaptation, resistance to adverse climatic conditions, and disease and insect resistance These characters must be taken into consideration, also, while developing varieties with better combinations of yield genes Since the crop is propagated vegetatively and can be maintained in the heterozygous state, the hybrid vigour of F_1 plants can be retained With clonal propagation the chance of genetic deterioration of a variety is minimized also

Breeding for Regional Adaptability. In India, potato growing areas have been grouped into six agroclimatic zones as follows (*1*) temperate hills with a single summer crop, (*2*) subtropical plains with two crops in autumn and spring, (*3*) subtropical plains with a single long duration winter crop, (*4*) tropical plains with a single short-duration winter crop, (*5*) plateau region with two crops during summer and winter, and (*6*) tropical hills where three crops during summer, autumn, and winter can be grown Breeding is in progress to develop varieties suited to growing in each of these areas

The relation of the photoperiod to the potato is complex In general, vegetative growth is favoured by long days and moderate temperatures, stolon growth is favoured by long warm days, while tuber yield is favoured by long days to stimulate vegetative growth followed by short days to activate tuberization [7] Tuber shape is also affected by day length, with largest tubers produced in long day conditions, but the smoothest and most uniform tubers are produced in short day conditions Varieties and species of potatoes differ in their photoperiod response The reaction to photoperiod is inherited and a large number of genes are involved, although the genes for short days appear to be dominant [7]

In the hills of north India, the potato matures in autumn under long day conditions, while in the plains of north India the crop matures in winter under short day conditions The nucleus seed for the short day crop in the plains is grown during long summer days in aphid free high altitudes at Kufri and Simla Hence, it would be preferable if the varieties for the plains would be day neutral The local Phulwa variety is day neutral and may be a source of genes for such a character Some of the long day adapted varieties, like Up to-Date, Craigs Defiance, and Hybrid 2236 respond well under short day as well as long day conditions Among the other species of *Solanum*, *S acaule*, *S demissum*, *S Antipovichii* and *S andigena* possess genes for adaptability to short days [36]

Another important aspect of regional adaptability is maturity Earliness is of value in areas where the favourable growing periods are short Further, early maturing varieties are also needed where two or more crops of potato are grown during the year Early maturing varieties are more economical in use of irrigation water Early varieties tend to escape aphid infestation when grown in autumn An early crop may escape frost injury or charcoal rot infestation in certain areas The growers prefer an early variety as the early crop brings a better market price Early maturing strains usually flower more sparsely than late strains and sparse flowering is often associated with high yield

Genes for earliness are present in species like *Solanum Rybinii*, *S phureja*, and a few introduced varieties of *S tuberosum* like Craigs Defiance The variety A 2708 developed by the Central Potato Research Institute from the cross S 4485 × Kufri Kuber is an early type Varieties maturing in about 110 days in the hills will normally mature in about 75 days in the plains, and are considered to be early in contrast to varieties requiring longer periods of maturity Generally, it has been difficult to combine earliness and late blight resistance in the same variety

Heat, Frost and Drought Resistance. Resistance to heat, frost, and drought are desirable to prevent losses when the potato crop is grown under these adverse climatic conditions

A RESISTANCE TO HIGH TEMPERATURE OR HEAT The development of a potato plant may be divided into three periods These are germination, growth, and tuberization Germination and growth are favoured by warm temperatures while tuberization is favoured by cool temperatures, preferably below 18 degrees Centigrade Normally, there is a reduction in size of tubers with temperatures above 18 to 20 degrees Centigrade during the tuberization period and practically no tuberization takes place with temperatures above 29 degrees Centigrade In most areas of south and southeast Asia, tuberization would be improved if varieties tolerating higher

temperatures during tuber formation could be developed

Breeding materials may be screened for heat resistance by testing for (*a*) foliage resistance to high temperature and (*b*) tuberization during high temperatures In testing for foliage resistance at the Potato Research Institute, plants are kept in an oven at 50 degrees Centigrade for 8 hours during the night for a period of 14 days Extremely susceptible varieties will generally collapse within 3 days under these conditions In testing for tuberization, the plants are kept in a glasshouse at temperatures of 30 to 38 degrees Centigrade during the tuberization period and then compared for amount of tuber formation Root knot nematode and charcoal rot are generally problems in heat affected areas and screening for them may be carried out while testing for heat resistance Tests at Simla indicate that certain potato clones such as H B 827, H B 841 and H B 858 are tolerant to high temperatures besides being good yielders [50] Certain clones of the diploid wild species, *Solanum chacoense*, are also reported to possess genes for resistance to high temperature [38] Crosses of *S tuberosum* have been made with artificially induced tetraploids of *S chacoense*

B FROST RESISTANCE In certain areas, like western Uttar Pradesh, Rajasthan, and Punjab in India and in northern Pakistan the potato crop grown in the autumn may be injured by frost before tuberization is completed Varieties that can tolerate frost would be desirable for such areas Screening for frost resistance is carried out in freezing chambers as well as in the field in the areas where frost occurs A detached leaf technique may be used for quick and large scale screening for frost resistance [50] In this technique leaves of the potato are exposed to a temperature of about −5 degrees Centigrade for 8 hours The leaves from susceptible varieties lose their turgidity and glossiness and become discoloured due to osmosis from the chloroplasts, effects which can be observed immediately

The tuber bearing species *Solanum curtilobum S acaule*, and others have been reported to be frost resistant [29] Screening tests at Simla indicate that the hybrid clones C 3745, C 3975 and C 3804 are frost resistant [43] These three hybrids are selections from the cross, Craigs Defiance × Kufri Safed

Breeding for earliness may enable the potato crop to escape damage from late frosts in autumn seeded crops

C DROUGHT RESISTANCE Drought resistance in potato is desirable when the potato is grown in autumn in areas where there are no irrigation facilities or where irrigation facilities are inadequate Screening for drought resistance can be done either in the field or in pots under drought conditions

Breeding for Disease Resistance. The potato in south and southeast Asia suffers from a number of diseases The important diseases are late blight, charcoal rot, wart, early blight, and viruses Besides these diseases, brown rot, scab, and wilt are also fairly common in some areas

Breeding for disease resistance is complicated by (*a*) the need for developing resistant varieties for so many agroclimatic areas, and (*b*) the presence of different physiologic races of the many pathogens in the different areas

A LATE BLIGHT Late blight, caused by *Phytophthora infestans* (Mont) de Bary, is a serious disease of the potato crop [6 61] Late blight may be spread by planting infected tubers or by wind blown spores in the field It is present in the hills of north India in summer, prolonged wet and warm weather favouring infection In the plains it develops during the winter but the period of infection is not as long as in the hills Three physiologic races of the fungus, 0, 1, and 4 have been reported so far in India [9] Race 0 is dominant in the northern plains Races 0 and 1 have been found in the northern hills Races 0 and 4 have been observed in the hills of Assam Race 1 has been found in the Nilgiri hills of south India In Europe and America the physiologic race pattern is much more complex than that found so far in India [1 2] Breeding is further complicated because foliage resistance and tuber resistance may differ in the same variety

Two types of resistance are recognized, (*a*) *field resistance* and (*b*) *immunity* [6 61] *Field resistance* is a general type of resistance where a variety can withstand moderate infection by different races of the pathogen In a variety with field resistance the pathogen requires a longer period of time to sporulate and produces a smaller number of spores than in a susceptible variety Thus moderate protection is offered for a limited period of time against a complex of races Inheritance of field resistance is polygenic and controlled by many genes *Immunity*, on the other hand, is the specific resistance of

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a genotype to a particular physiologic race of the pathogen [26] Immunity to a specific race is usually inherited as a single dominant gene It is more difficult to accumulate genes for field resistance into a variety than to transfer single genes for immunity, but field resistance is more lasting than immunity since the protection offered through an immune variety may be breached by a single gene mutation, or other gene change, in the pathogen The changed pathogen may then infect the previously immune variety Vander Plank has used the terms horizontal and vertical resistance to denote the broad, polygenic inheritance of field resistance and the specific, oligogenic resistance of immunity [62] He emphasizes that horizontal resistance slows down the rate at which disease increases in the field and vertical resistance reduces the amount of inoculum which starts the infection The vertical resistance (genes for immunity) should be used to supplement horizontal (field) resistance but not to replace it Similar observations have been made with the cereal rusts, diseases caused by fungal organisms which are highly specialized and possess many physiologic forms or races

Resistance to late blight is found in several wild species of *Solanum*, but *S demissum* has been used as the primary source of resistance because it crosses more easily with the *tuberosum* species and the wild characters may be more easily removed from the crosses [1 28 29 45] In Europe several major genes, designated R_1 R_2 R_3 R_4 etc , have been identified in differential varieties and are used to identify the specific physiologic races of the blight pathogen [2] In India, resistant lines from Scotland, U S A , and Mexico are being used as sources of resistance Most of the resistant lines have *S demissum* genes for field resistance and immunity Genes for field resistance have been found in *S andigena* also The goal at the Central Potato Research Institute is to combine genes for field resistance with genes for immunity

Screening of seedlings for resistance to late blight may be done both in the laboratory and in the field In the laboratory small filter paper disks dipped in spore suspensions of the late blight organism are placed on detached leaflets and the leaflets are incubated in moist chambers until sporulation develops on the leaf Detached leaves may also be treated with hormones to induce rooting [53 60] The rooted leaves will continue to grow in the glass house in soil for a sufficient length of time to be used in tests for resistance Both procedures permit the plant to continue growing in the field while the test for blight resistance is being made In the field, screening can be done in areas where the disease is known to occur by planting the materials to be tested along with known susceptible and resistant varieties Screening of varieties in the field has its limitations as evaluation for resistance is made only to the specialized races present in the field Since field resistance cannot be observed if the strain carries at the same time genes for immunity to races present in the field arrangements have been made with the Scottish Plant Breeding Station in Scotland and the Rockefeller Foundation in Mexico to test breeding materials developed in India in the field at these locations where a large and virulent group of physiologic races of the late blight organism are usually present [28] Another problem in breeding for blight resistance is that resistance in the leaves and tubers is inherited separately in some varieties [57]

B VIRUS DISEASES Several viruses infest the potato crop These are virus X, virus A, virus Y, leaf roll virus S, virus C, and spindle tuber, as well as several soil borne viruses Virus C is closely related to virus Y Virus X, virus S, and spindle tuber are transmitted by contact Virus Y and leaf roll are transmitted by aphids In India breeding work has been concentrated on resistance to viruses X and S which are transmitted by contact since control of virus Y and leaf roll is possible by growing seed potatoes in an aphid free environment [39]

Virus X is the most widely distributed virus of potato and is present throughout south and south east Asia as well as Europe and America There are many strains of the virus and three types of resistance have been reported [3 41] These are (*a*) resistance to infection, (*b*) hypersensitivity or field immunity, and (*c*) extreme resistance or immunity The latter two are used mostly by the breeder, however, the immunity type of resistance is generally preferred [20] Hypersensitivity is controlled by a single dominant gene *Nx*, inherited in a tetrasomic pattern [3] Another gene, *Nb*, has been described for field immunity to the strain B of the X virus Two other genes, *Ne* and *Nr*, have also been reported for hypersensitivity Four genes for immunity have been described In the case of U S seedling 41956, a much used source of resistance, immunity is deter-

mined by two dominant complementary genes *A* and *B* In *Solanum acaule* and *S andigena*, a single dominant gene *Rx* controls immunity Yet in another case of a selection of *S tuberosum* from Wisconsin, immunity is reported to be controlled by a gene *C* in the recessive homozygous condition [20] Thus genes for immunity are now available even in the cultivated types of potato

Screening for virus X at the Potato Research institute, Simla, is done in several stages Initially the seedlings are grown in flats or boxes and sprayed with a suspension of virus X grown on tobacco leaf Susceptible seedlings are rejected and the remainder are planted in pots The potted plants are then inoculated by introducing the virus mechanically by abrasion and checked for resistance The next step is to graft an infected scion of tobacco or *Datura* onto a stalk of potato observed to be resistant in previous tests After two days the test for virus in the potato is made, either serologically, or by inoculation of an indicator plant, like *Gomphrena globosa*, with sap from the grafted potato stalk The latter test is required to identify latent virus in the potato, symptoms of which cannot be identified except by serological tests or by the graft test

Field immunity for virus A is controlled by one gene *Na*, which is stated to be closely linked with the gene *Nx*[17] making it possible to breed for resistance to both races at the same time The gene *Na* is in several commercial varieties and in the wild species *Solanum chacoense* and *S demissum* The hypersensitive type of resistance has been reported for virus Y [36] At Simla, resistant clones have been obtained from Scotland, U S A , Netherlands and West Germany In virus C, which is closely related to virus Y, hypersensitive resistance is controlled by one gene *Nc*,[19] which is also linked with the *Nx Na* complex [17]

Leaf roll is another virus of potato that is prevalent throughout south and southeast Asia. Control is complicated by the fact that the aphids which carry the infection can retain their infective power throughout their lifetime Resistance to leaf roll is believed to be controlled by a large number of genes with cumulative effect The varieties Shamrock, Southesk and Imperia are resistant [36]

Virus S is carried either symptomlessly or with a mild mottle This has been reported in India only recently The varieties, Saco and Tewa, from the U S.A are sources of resistance

C CHARCOAL ROT Charcoal rot is caused by *Macrophomina phaseoli* (Maubl) Ashby It is prevalent in the plains of India, and infection occurs when potatoes are grown in high temperatures The disease later develops in the stored tuber [30] At the Central Potato Research Institute, clones of *S chacoense* have been found to be resistant [31] These clones are also of interest because they have the ability to tuberize under high temperatures and are now being used in breeding programmes Inoculation for charcoal rot may be done by inserting toothpicks containing the organism into tubers The tubers are incubated at temperatures of 32 to 34 degrees Centigrade and the extent of development of the disease in the tuber is observed in comparison with that in susceptible check varieties

D POTATO WART Potato wart, caused by *Synchytrium endobioticum* (Schilb) Percival, has emerged as an important disease in the Darjeeling hills of India Varieties resistant to wart have been developed in the U K U S.A , and the Netherlands,[25 43] and these varieties have been utilized at Simla as sources of resistance Resistance is also found in several wild species [25] Testing is being done at a field station established in the area of infection so that the disease will not be carried to other parts of India.

E EARLY BLIGHT *Alternaria solani* (Ell and Martin) Jones is a fungus causing early blight which occurs in both the hills and the plains of India Screening of existing varieties and species indicates that some varieties like Maritta possess resistance to early blight Some wild species are also resistant to the disease [49]

Insect Resistance. Important insect pests of potato include nematodes, aphids, and *Epilachna* beetle Attempts at breeding resistant varieties have been primarily aimed against nematodes and aphids

The root knot nematode, *Meloidogyne incognita*, is the most important nematode on potato In the Nilgiri hills in south India the golden nematode, *Heterodera rostochiensis*, is common also To screen for resistance in the laboratory, potato tubers are sprouted in small pots with sterilized soil into which several hundred larvae are released one week after planting Pots are kept at a temperature near 25 degrees Centigrade and the roots are scored for nematode damage after 75 days [51] The leaf culture

technique discussed earlier may also be used for this purpose In the field, screening may be done by growing the materials in areas known to be infested with nematodes along with susceptible varieties as checks The hybrid H G 294, a selection from the cross Kufri Red × (Gladstone × Tab orky), has been reported to be resistant to *M incognita* This hybrid also is resistant to high temperature and drought conditions prevalent in nematode infested areas [19] In Europe physiologic races of the potato root eelworm, *H rostochiensis* have been reported and resistance observed in *S andigenum S vernei*, and some other wild species [8]

More than ten different species of aphids are recorded on potato in the different areas of India Of these *Myzus persicae* Sulz is the most important The resistance of potato varieties to aphids appears to be associated with the hairiness of the leaves Aphid resistance would also help to give protection to virus diseases transmitted by aphids

The most common potato beetle is *Epilachna ocellata* A few wild species of *Solanum* like *S Garcetae*, *S malinchense*, and *S polyadenium* are reported to be resistant to this beetle [43 31]

Quality Better quality of the potato tuber helps to ensure consumer acceptability and a better premium in the market Of the various desirable qualities of the tuber mention may be made of keeping quality, cooking quality, seed size, shape, colour, texture, skin thickness, nutritive value, and position of eyes

In order to produce virus free nucleus seed, it is the practice to produce potato seed at high altitudes which are relatively free of aphids, or in the plains in autumn during periods of low aphid infection In either case seed is often stored for long periods and used to plant next autumn's crop It is important that the tubers have good keeping quality and do not degenerate in storage, either in viability in the case of seed, or in nutritive value, in the case of potatoes to be used for food Some local varieties, like Phulwa, can stand storage conditions for longer periods with less deterioration than other varieties Keeping quality is associated with non sprouting and resistance to storage diseases [36] *Solanum chacoense* also is reported to have good storage qualities

Varieties differ in their cooking qualities, some requiring prolonged cooking while others cook easily Freedom from after cooking darkening is also desirable Seed size and shape are primarily a question of consumer preference Round shaped potatoes are preferred and sell for a better price in certain areas Small tubers are not generally preferred for marketing, however, large sized potatoes create problems in seed production since the whole potato is planted in India to reduce disease infestation and a large potato requires that more seed be planted Uniform and medium sized potatoes will be preferable from all considerations White tubers are preferred to red ones and they sell at higher prices in most markets Thick skinned varieties have several advantages over thin skinned ones The former will stand harvesting, handling, and transportation with less damage Thick skinned potatoes also possess better keeping qualities Little attention has been given to breeding tubers with better nutritive value, especially tubers rich in protein content and vitamins Varieties with shallow eyes are preferred by consumers as there is less loss in preparation of the tuber for cooking but deep eyes in seed potatoes afford protection for the growing tip

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14

Breeding Jute

Jute is second only to cotton as a source of plant fibre Jute fibre is extracted from the bark of the jute plant and is known as a bast fibre in contrast to the seed fibre from the cotton plant About 95 percent of the world's jute is produced in India and Pakistan,[17 21] and jute fibre is a major item of export from these two countries Jute fibre is the lowest priced of the important textile fibres and is used in the manufacture of cordage, gunny cloth, gunny bags and other packaging materials for agricultural and industrial products Although wild jute has been harvested since very early times, the cultivation of jute in India did not begin until the early part of the nineteenth century

ORIGIN AND CLASSIFICATION

Jute belongs to the genus *Corchorus*, in the family *Tiliaceae*, or lime family The genus *Corchorus* contains about 40 species which are distributed throughout the tropical regions of Africa, South America, Australia, China, and southeast Asia [21] Only two of the species, *Corchorus capsularis* and *C olitorius*, are cultivated for their fibres (Fig 14 1) Of the three million acres of jute in India about 75 percent is planted to *C capsularis* and the remainder to *C olitorius* The generic name *Corchorus* is believed to have been derived from the word "Korkhoros" used by the Greeks to describe a pot herb, possibly *C. olitorius* [21]

The greatest diversity of species of *Corchorus* is found in Africa where 36 of the 40 known species have been recorded Next to Africa, 8 species may be found in India with races of *capsularis* most numerous The centre of origin of the *capsularis* species is believed to be in the Indo-Burma region of southeast Asia [15 21] Although *C capsularis* is not found in Africa, a large number of races of *olitorius* is found there and Africa is the primary centre of origin of the *C olitorius* species with Indo Burma as a secondary centre of origin [18 21]

An extensive survey of the jute growing areas in India was made in the early part of the century to determine the kinds of jute being grown Based on morphological characteristics of the plant, colour markings of stems and flowers, maturity, and chemical properties of the fibre, 33 distinct types of *C capsularis* were described, 30 of which were grown for fibre and 3 as vegetables Five types of *C olitorius* were described [24] Later studies at the Jute Agricultural Research Institute indicate more than 70 races or types of *capsularis* and at least 12 races or types of *olitorius* have been identified [20]

BOTANY AND GENETICS

Although the two cultivated species of jute, *Corchorus capsularis* and *C olitorius*, are alike in general appearance there are considerable differences between them in height, leaves, flowers, pods, seeds, fibre colour and fibre quality [9 19 21] *Corchorus capsularis* is shorter and has smaller leaves and smaller flowers than *C olitorius* The leaves of *capsularis* have a bitter taste while those of *olitorius* are tasteless The seed pods of *capsularis* are globular or pear shaped while those of *olitorius* are long and cylindrical (Fig 14 2) The seeds of *capsularis* are chocolate brown in colour Seeds of *olitorius* are smaller than those of *capsularis* and bluish green to steel gray or even black in colour (Fig 14 3) The fibre of *capsularis* is whitish in colour and is known as "white jute" in commercial trade The fibre of *olitorius*, sometimes known as "tossa" by the trade, is yellow to grey or even reddish in colour and is finer, softer, stronger, and more lustrous in colour than the fibre of *capsularis* Both species have a tap root but the root system of *capsularis* is shorter and more branched [16] This probably affects the adaptation of the two species since *capsularis* grows on all types of land, low or high, but *olitorius* cannot stand waterlogging and is grown only on high lands not normally in-

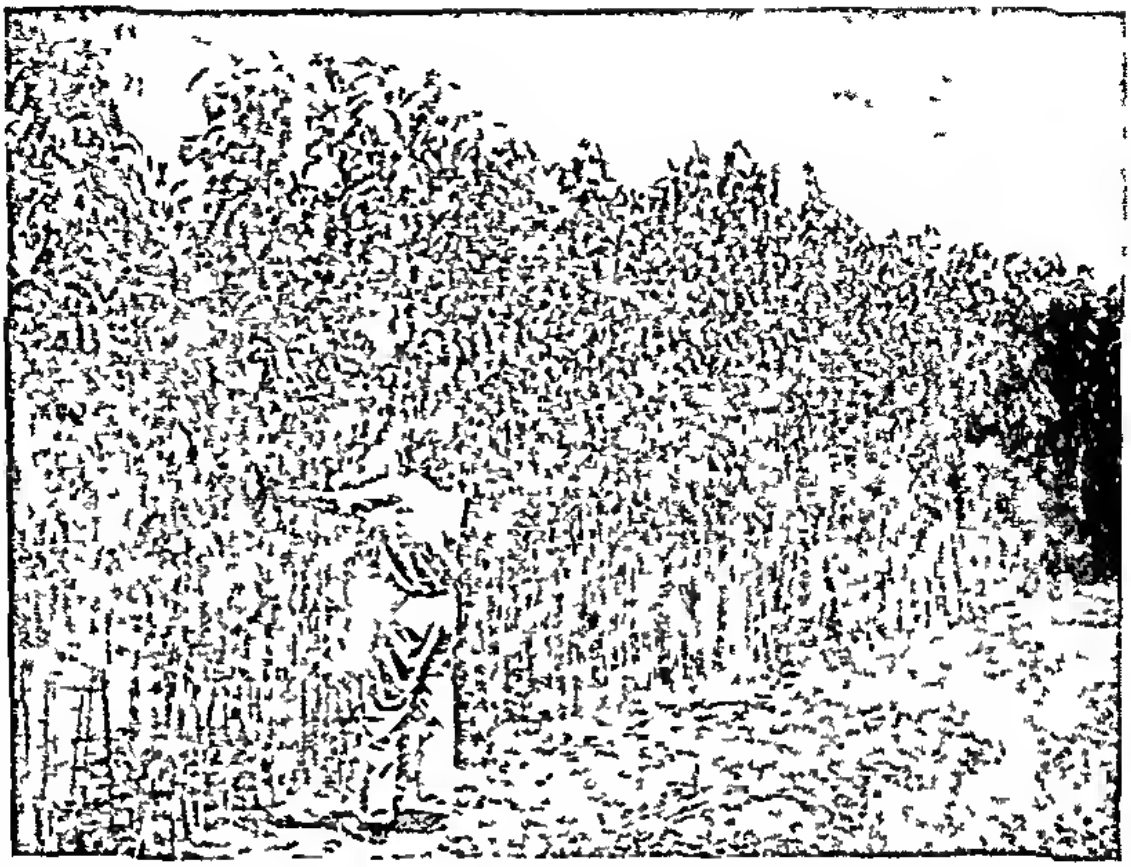


Fig 14 1 *Capsularis* jute growing on the Jute Agricultural Research Institute Farm Barrackpore, India

undated *Capsularis* can be grown profitably with early February and March plantings, while plantings of *olitorius* are made only from mid April until June, since early plantings of *olitorius* result in premature flowering and lower yield

The inflorescence in both species is a condensed cyme opposite the leaves with a group of 2 to 5 flowers The flowers have five sepals and five petals In *capsularis* the flower is 0 3 to 0 5 cm in length and has 20 to 30 stamens, whereas in *olitorius* the flower is about 1 cm in length and has 30 to 60 stamens (Fig 14 4) The seed pods in both species, the globular fruits of *capsularis* and the cylindrical fruits of *olitorius*, produce numerous small seeds

Anthesis starts one to two hours after sunrise in *capsularis* and about an hour before sunrise in *olitorius* The stamens usually burst before anthesis and self pollination is the rule in both species, although natural cross pollination, averaging 2 to 3 percent in *capsularis* and 10 to 12 percent in *olitorius*, normally occurs [5 9 27] The higher rate of natural crossing in *olitorius* may be due to the larger size of the flowers and to their remaining open for a longer period of time [10] The natural crossing is the result of both wind pollination and insect visitation [27]

The diploid chromosome number in both *C capsularis* and *C olitorius* is $2n = 14$ The basic number in the wild species of *Corchorus*, as well as the cultivated species is $n = 7$ [1 12] *Corchorus siliquosus*, *C hirtus*, and *C pilolobus*, wild species, are tetraploids each with a chromosome number of $2n = 28$ [12 26 52]

Selfing and Crossing Techniques. To ensure self fertilization the flowers may be protected by covering them with fine mesh muslin bags or a polyethylene lantern (Fig 14 5) This is necessary in the *olitorius* species where cross pollination is much higher than in *capsularis*, but in the *capsularis* species, in which cross pollination is relatively low, the flowers are not generally bagged in breeding experiments, the natural crossing being ignored Since plants of jute are rather tall, with the inflorescence mostly at the top of the plant, it is necessary to support the bag covering the flowers with a bamboo stake, or by a bamboo framework or scaffolding if a number of plants are to be protected The bags may be fitted with bamboo rings or cages to prevent the walls of the bag from

Fig 14.2 Seed pods of jute Seed pods of *Corchorus ol torus* (left) are cylindrical n shape while those of *C capsula is* (right) are globular or pear shaped

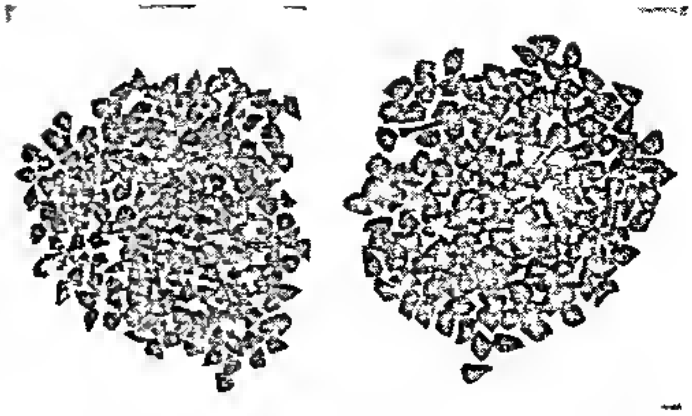


Fig 14 3 Seeds of jute Seeds of *C ol torius* (left) are smaller than those of *C capsularis* (right)

Fig 14 4 Flower of *C ol torius*

collapsing and injuring the flowers (Fig 14 5) [10]

Cross pollinations between varieties within a spec es are readily made but interspecific crosses are rarely successful Emasculation is done one day ahead of the opening of the flowers [10] Normally the first bud to open in an inflorescence is emasculated and the other buds removed The most advanced bud in the inflorescence can be recognized from its size and from the yellow colour of the petals and anthers as compared to whitish petals and reddish anthers in the immature buds The bud selected is opened and the stamens removed with fine pointed forceps (Fig 14 6) Extreme care must be exercised not to injure the flower as the jute flower is very sensitive to the removal of petals or sepals The emasculated flowers are covered with small butter paper bags to protect them from the dew and rain

Pollinations are made the following morning up to about 9 30 A M in the case of *olitorius* or up to around 11 00 A M in the case of *capsularis* [10 21] The stigma of the emasculated flower is lightly touched with a ripe anther so that the stigma is covered with pollen After pollination the flowers are bagged for 24 hours at which time the bag may be removed The success of the pollinations may be observed 3 to 4 days later by examination of the ovary with a hand lens as unfertilized capsules will be shrivelled and discoloured Seed pods mature in about 6 weeks and should be collected promptly before they shatter and the seed is lost

Genetic Studies A number of genetic studies have been made on jute Mostly these studies in clude anthocyanin pigmentation pod characteris tics like shape size surface and cluster habit, branching habit leaf characteristics flower colour, and others [19 21] Presence of anthocyanin pigmenta tion is useful as a marker in identifying strains of jute Three loci are involved in the production of anthocyanin patterns Branching habit in capsu

Fig 14 5 Flowers of jute plant protected from cross pollination by a muslin bag fitted over a bamboo cage which is supported by a bamboo pole

laris is controlled by a single gene, *BrBr* The recessive gene br for non branching is found only in some exotic varieties The Indian *capsularis* jutes have long branches while short branches are found in some Chinese varieties Length of branches is reported to be controlled by duplicate factors Crosses of oval and round podded varieties of *capsularis* produce pods of intermediate shape in F_1 with simple monogenic F_2 ratios Very little is known about the inheritance of most economic characters of the jute plant utilized in breeding

BREEDING METHODS

Breeding procedures used in jute have been mainly selection and hybridization as practiced in self-pollinated crops While jute has considerable cross-pollination, particularly in *C olitorius*, selfing in breeding material may be enforced by bagging

Fig 14 6 Emasculation of flower bud in *capsularis* jute

and protecting the jute flower from wind or insect pollination as previously described The role of introduction, selection, hybridization, radiation breeding and polyploidy are discussed here

Introduction and Germ Plasm Collections. Since jute is primarily of Indo Asian origin and since India and Pakistan are the principal areas where jute is cultivated, introduction has not played the important role in breeding that it has in some other crops The importance of collecting local types to use as breeding materials was recognized quite early in the jute improvement programme in India In the early years of the 20th century a survey of the jute growing areas in India was made and jute types growing in the areas collected [24] From these collections the first selection work with jute was initiated [6] More recently, introduced or exotic varieties have been used also in selection and hybridization [25] The variety JRC 206 (Jute Research *capsularis*) has been developed as a selection from a Brazilian type JRO 7835 (Jute Research *olitorius*) is a very promising type selected from a cross between a local strain, JRO 632, and an exotic variety, Sudan Green, obtained from Sudan, Africa A collection of about 60 *capsularis* and 20 *olitorius* types, of which about one-fourth is introduced or exotic types, are now being maintained at the Jute Agricultural Research Institute in India

Selection. Pure line selection has been the primary method of improving the jute crop [6] Kakya Bombai, a *capsularis* type distributed in 1916, was the first improved variety to be developed in India Kakya Bombai was selected from a local type D 154, selected from Kakya Bombai in 1919, was

less susceptible to chlorosis and more resistant to stem rot than Kakya Bombai D 38, an *olitorius* type later known as Chinsurah Green, was selected from a local strain from Chinsurah district in about 1915 For many years D 154 (*capsularis*) and Chinsurah Green (*olitorius*) were the standard types in cultivation Chinsurah Green matured in about 105 days and was one of the earliest varieties in the *olitorius* group Two other *capsularis* varieties developed by pure line selection that deserve mention, owing to their widespread cultivation, are JRC 212 and JRC 321 JRC 212 was selected in 1939 from local materials Its maturity is the same as that of D 154 but the yield is much higher than the latter JRC 321, selected in 1942 from a local material called Hewti, yields much higher than D 154 Further, it is early and suitable for growing in low lying, double cropped areas to be followed by winter rice In the *olitorius* group, JRO 632 and JRO 753, selected in 1940, have given much higher yields than Chinsurah Green [21]

Hybridization. Hybridization is used to combine desirable characteristics of two or more parent varieties Hybridization was first used for the improvement of jute in India in 1910 [24] However, systematic attempts at hybridization did not begin until 1917 About 1940 a series of multiple crosses was started at the Jute Agricultural Research Station then located in Dacca No varieties of record emerged from this early hybridization work Hybridization has since been resumed at Dacca and at the new Jute Agricultural Research Institute near Barrackpore in West Bengal In 1956 57 a large number of crosses were made at Barrackpore with the objectives of disease resistance, early maturity, lodging resistance, and high fibre yield Some promising selections have been made from these crosses Many of the crosses involved exotic varieties like Russian Red, Russian Green, Sudan Green, Japanese Green, Liza Fanduk, and others Before a successful hybridization programme can be initiated in any crop it is necessary first to identify useful genes in available varieties which may then be used as parents in crosses As more information is accumulated on sources of genes and their inheritance, the backcross may be used to concentrate genes for a particular character, or to add a specific desirable gene to an adapted variety

A INTERSPECIFIC CROSSES Desirable genes for specific characters like disease resistance are often found in related wild species even though they may not be present in the cultivated species In such cases the genes may be transferred to the cultivated species, if interspecific crosses can be made successfully, and utilized in the breeding programme In jute the two cultivated species *C olitorius* and *C capsularis* each have desirable characters that would complement the needs of the other species *C olitorius* has stronger and more lustrous fibre but *C capsularis* has a wider range of adaptation as it can be sown either early or late, or on high land, or in water-logged conditions As early as 1912, Finlow reported that races of *olitorius* or of *capsularis* could be crossed among themselves but would not cross with races of the other species [21] Since then many attempts have been made to hybridize these species but, until recently without any success [23 24] If the ovules were fertilized the seeds set were usually shrivelled or empty and would not germinate A primary cause for the failure to obtain viable seeds after fertilization of the ovule appeared to be the abortion of the young embryos [8]

Many techniques have been tried in attempts to overcome these failures and bring about success in crosses between the *olitorius* and *capsularis* species [21] These have included smearing of the stigma of the female parent with a stigmatic exudate from the pollen parent reducing the length of the style, use of mixed pollen cross pollination followed by self pollination after a few hours crossing at diploid × tetraploid or at tetraploid × tetraploid level, hormone application to reduce fruit drops after fertilization and crosses among scions of interspecific grafts

Indole 3 acetic acid is a hormone used to prevent drop of flower buds in fruit crops Following reciprocal crosses between the two cultivated jute species, the flower pedicels in one experiment were treated with indole 3 acetic acid Fifteen fruits and 365 seeds were obtained in 115 crosses of which 7 seeds germinated and 3 hybrid plants grew to maturity [13 14] The F_1 hybrids, all of which came from crosses in which *olitorius* was used as the female parent, were weak but showed some characteristics of each parent The F_2 and F_3 generations were stronger and segregated for some characteristics but had mostly fruits of *olitorius* type In a later experiment, using hormone applications and embryo culture, seeds were obtained from the reciprocal cross using *capsularis* as the female parent

One hybrid plant grew to maturity but dropped its flowers [11]

Some success has also been attained in crosses between the species when crosses were made between pollen and seed parents, each of which had been grafted on to the other species [33 36] In the cross of *C olitorius* as the female parent and pollinated from *C capsularis*, F_1 plants were intermediate in phenotype, but F_2 and F_3 populations had a preponderance of plants which approached *C olitorius*, the mother plant, in appearance No plants had the globose fruits of the *capsularis* parent

These experiments have not yet solved entirely the breeders' problem of combining the desirable characteristics of the two cultivated jute species However, they do give hope that the incompatibility barriers may some day be more completely understood and that recombinations between the species are not impossible as was indicated for many years

B HYBRID VIGOUR Hybrid vigour apparently has been given very little consideration in the breeding of jute Two considerations make it appear desirable to investigate the utilization of hybrid vigour in the jute crop, (*a*) Increased size and vigour of a hybrid plant would contribute to the yield in jute, fibre yield in this crop being closely correlated with plant size (*b*) Partial cross pollination in *olitorius* jute makes it appear that adequate seed production might be obtained in a male sterile form of this species The utilization of hybrid vigour would require finding cytoplasmic male sterile types or other suitable means of controlling pollination which are not now available Fertility would not need to be restored to jute planted and harvested for fibre production

Mutation Breeding. X radiation and gamma-radiation studies with jute have been carried out at the Jute Agricultural Research Institute in India and elsewhere [3 15 21 22] A number of mutant selections have been made from irradiated populations and are being carried forward Some desirable characters like disease resistance, drought resistance and higher yield are reported to have been isolated by selection from the irradiated populations although the mutant strains may not be suitable for release without further breeding Most of the observed mutants following irradiation are aberrations in morphological characters of the plant which are not useful to the breeder

Polyploidy. Polyploidy in jute would be useful if plant size and fibre content could be increased and seed production is not impaired too seriously However, polyploids developed thus far have not led to increase in fibre content and there has been a marked decrease in seed set [2 4 15] Tetraploid lines of the varieties D 154, JRC 212, JRC 919, Chinsurah Green, JRO 632 and wild *olitorius* have bee established

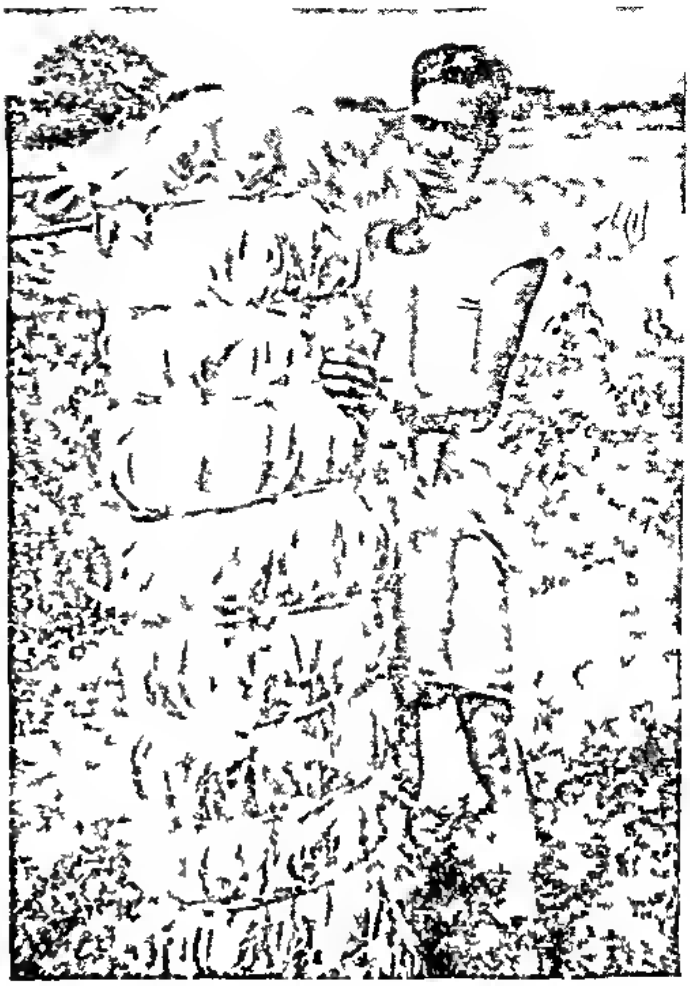
Jute Agricultural Research Institute. Improvement of jute in India began in 1904 whe the Bengal Department of Agriculture appointe Mr R S Finlow as fibre expert [7 20 21] The fir variety to come from this work, Kakya Bomba was distributed in 1916 The two high yieldin strains D 154 (*capsularis*) and Chinsurah Gree (*olitorius*) were later products of Mr Finlow's worl In 1936 the Government of India established th Central Jute Committee and a Jute Agricultur Research Laboratory was started at Dacca in 1939 With the partition of India in 1947 the work of the Laboratory was interrupted, but a new Jute Agricultural Research Institute was established in India in 1948 and moved to Barrackpore, West Bengal in 1953 Recently the breeding work on jute in India was extended to develop varieties suited to the jute growing states of Assam Bihar, Orissa, and Uttar Pradesh, as well as to West Bengal The improved *capsularis* varieties developed by the Jute Agricultural Researeh Institute are named by giving them the letters JRC (Jute Research *capsularis*) followed by a number Similarly, the *olitorius* varieties are given the letters JRO followed by a number The Jute Research Institute has also been reestablished at Tejgaon, Dacca, East Pakistan

OBJECTIVES IN BREEDING JUTE

The economic product of the jute crop is the bast fibre that is obtained from the bark of the plant (Fig 14 7 A and B) In this respect it is different from the other field crops like cereals, pulses, or oilseeds, where the economic product is the seed, and even different from cotton where the product is the seed and the attached fibres It also differs from crops like potatoes and sugarcane because, unlike those crops, seed production is also essential for propagation of the crop The principal objectives in breeding jute are, however, not different from those of other crops The main objectives of breeding can be discussed here under (*a*) yield, (*b*)

14 7A

Fg 14 7 A Removing jute fibre from the wood B Jute fibre ready for the market



14 7B

maturity (*c*) lodging resistance (*d*) disease resis tance (*e*) insect resistance and (*f*) fibre quality

Breeding for Yield Yield of jute fibre is depen dent both on the total weight of the plants harvested and the fibre content of the plant Plants of large size are necessary to obtain high gross yields per hectare of land area Fibre content of the jute plants varies from 4 5 to 7 5 percent with an average of about 5 5 percent [20] The breeder must therefore select plant types that will give the largest gross we ght and the highest fibre content

The jute plant reaches the proper stage of fibre maturity long before the seeds mature Retting and fibre extraction become difficult and both quantity and quality of fibre are reduced if harvesting is delayed until the seeds mature Thus no seeds are obtained when the plants are harvested for fibre at the proper time for fibre production Thus poses a special problem for the breeder in evaluation of his breeding material for fibre yield For, while it is desirable to measure individual plant selections for fibre yield which would require their being harvested before seeds are formed it is also neces sary to harvest seeds of the selected plants in order to maintain the strains To avoid destruction of the plant before the seeds can be harvested it has become the practice for breeders in early stages of breeding to evaluate yield from morphological characters that have a direct relation to fibre yield He ght and diameter of the base of the plant have been found to have a high pos tive correlation with fibre yield By comparing the measurements of height and base diameters in different plants the potential yields of the plants may be compared [10 21] Recently the fibre/wood ratio has been utilized also in yield evaluation [15 28]

A new technique of vegetatively propagat ng a part of the jute plant has been developed recently which may aid the breeder with the seed production problem If the top of the jute plant is cut off when the plant is about three months old and before the plant has flowered and the tops rooted the top will continue to grow and produce normal seeds in quantity [29 31] This practice will greatly help the jute breeder as it will perm t him to harvest a plant selection and measure its fibre quality and yield while still saving seeds from the selected plant

Breeding for Early Maturity The *capsularis* varieties of jute can normally be so vn between the end of February and the beginning of April while

the *olitorius* varieties can be sown from the middle of April up to the end of June With an early harvested crop, *capsularis* can be profitably grown in double-cropped areas and be followed by rice Breeding for early maturity would facilitate this practice With present varieties double cropping with rice is not possible with *olitorius* as it cannot be planted as early as *capsularis* However, early varieties are also desired in the *olitorius* species to grow in early rainfall or irrigated areas

Earliness and high yield are not necessarily compatible characteristics Early varieties tend to be short and late varieties tend to be tall [30] It may not be possible to combine highest yield with extreme earliness Early varieties tend to have superior fibre quality Fanduk, a *capsularis* variety, and Sudan Green, an *olitorius* variety, are introduced varieties which have been utilized in breeding for earliness

Breeding for Lodging Resistance. Lodging in jute may result from the bending or breaking over of the jute plant due to weak stems, a weak root system, or injury to the stalk by disease or insects Under any of these conditions lodging may occur, usually following a high wind or heavy rain storm Breeding for lodging resistance may be directed toward improvement in any of these inherent weaknesses

Breeding for resistance to lodging in jute poses a problem which differs from breeding for lodging resistance in cereals In cereals the primary aim is to shorten and stiffen the straw While in jute it is desirable to breed for stiffer stems, but shortening the plant would tend to reduce fibre yield, so plant height cannot be sacrificed unless high fibre yield can be retained On the other hand, plants too tall will lodge with a depreciating effect on quality and yield Thus selection for lodging resistance should include strong wood, a strong root system, strong stems of sufficient height to maintain high fibre yield, and resistance to stem and root rot diseases Plant height of 12 to 14 feet in *olitorius* and about 10 feet in *capsularis* types appears to be desirable for reasonable strength and high yield The variety Sudan Green is being utilized as a source for lodging resistance in *olitorius* [15]

Breeding for Disease Resistance. The major diseases of jute are stem rot (*Macrophomina phaseoli*), soft rot (*Pellicularia rolfsii*), and anthracnose (*Colletotrichum sp*) [15 19] In addition there are several diseases of minor importance Breeding work for disease resistance has been mainly confined to stem rot resistance although varietal resistance to anthracnose has also been studied

The stem rot fungus, *Macrophomina phaseoli* (Maubi) Ashby, can produce seedling blight, stem rot, collar rot, or root rot in jute Screening of existing varieties, both local and exotic, and breeding for resistance is in progress at the Jute Agricultural Research Institute, Barrackpore The standard variety, D 154, and JRC 918, a selection from Brazilian material, are sources of resistance for stem rot [15] Screening of breeding material is done with natural infection The selections are normally grown in areas known to carry the disease A susceptible variety like JRC 412 is included on the border to serve as a check and also as a source of inoculum

Breeding for Insect Resistance. Insect pests of jute are the semilooper (*Anomis sabulifera*), jute apion (*Apion corchori*), mites (*Hemitarsonemus latus* and *Tetranychus bioculatus*), and jute stem girdler (*Nupserha bicolor* Thoms ssp *postbrunnea* Dutta) Screening of materials, so far carried out, has not shown any sources of resistance except for jute apion in which case a few selections are reported to be resistant [15]

Breeding for Fibre Quality. The quality of jute fibre may be affected by the variety, the environmental conditions in which the jute is grown, and the retting process [20 21 24] Characteristics of fibre that determine its quality include length of fibre, strength of fibre, colour, lustre, fineness, and freedom from faults such as knots and specks Of these strength, colour, and lustre are of primary importance All of these may be improved by breeding

Fibre quality of *olitorius* varieties is superior to that of *capsularis* varieties In general, early varieties have better quality than late ones Strength of fibre is perhaps the most important single component of quality Strength is measured as "breaking load" in pounds per unit length of fibre Silky and glossy fibre is preferred to dull coloured fibre A defect in quality known as knotty fibre is found in branching type varieties, so development of non-branching varieties is desirable

Testing and evaluation of fibre quality from different jute varieties are aided in India by the work of the Jute Technological Research Laboratories, Calcutta

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15

Breeding Tobacco

Although native to the Americas, tobacco is now grown extensively in all of the countries in south and southeast Asia Tobacco was introduced into India during the early part of the 17th century and is presently grown on an area of about 4 lakh hectares with a total production of over 3 lakh metric tonnes India is third among all countries in production of tobacco, the first two being the U S A and China [29] In order of acreage grown the principal tobacco growing states in India are Andhra Pradesh, Gujarat, Mysore, Maharashtra, Madras, Uttar Pradesh, Bihar and West Bengal About three-fifths of the total production is in Andhra Pradesh and Gujarat states About one fifth of the total production is exported Tobacco is also an important crop in Thailand, Pakistan, Burma, Ceylon, Indonesia and other countries of south and southeast Asia [24]

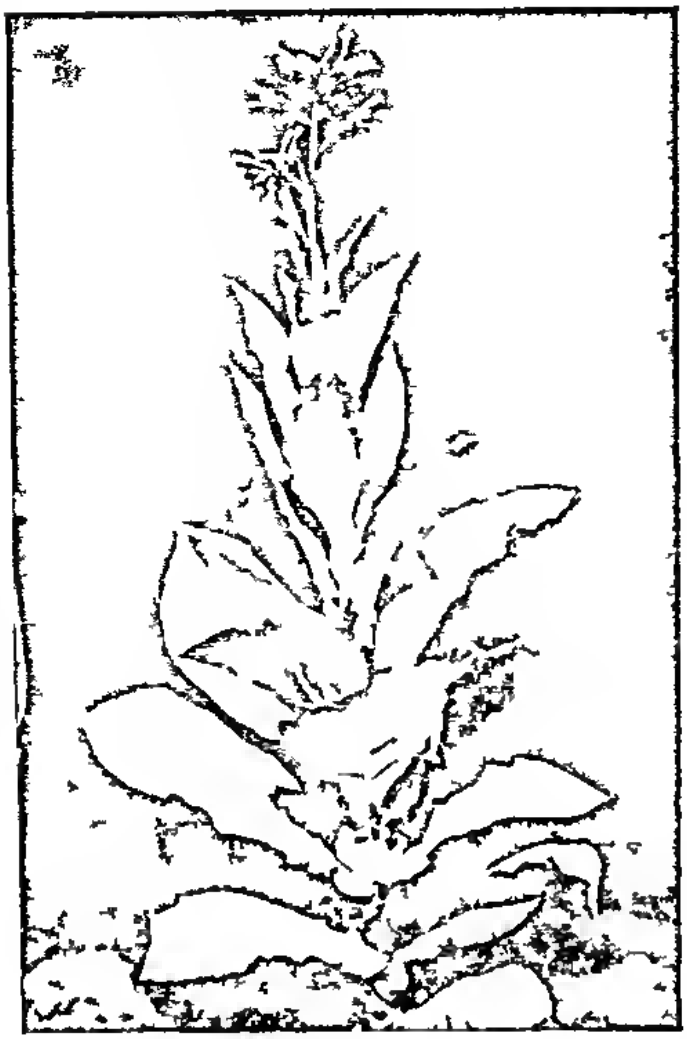
The kind and quality of tobacco grown is greatly influenced by the soil and the climate The tobacco leaf, which is the commercial product of the crop, develops its characteristic quality only under fairly precise environmental conditions Temperature and moisture are important climatic factors affecting the quality of the tobacco leaf As a result tobacco production tends to be concentrated in small areas and the tobacco produced in a specific area will have certain peculiar quality characteristics which distinguishes it on the market from tobacco produced in other areas [23] In India the crop is grown during the winter months when the mean temperature for the crop growth is between 21 and 32 degrees Centigrade and the relative humidity is high

Progress in breeding for yield and other characteristics is very much complicated by the fact that quality, which is of prime importance, is an elusive and complex trait that cannot be seen or measured quantitatively It is expressed only through such qualitative features as taste and aroma, and then only after the tobacco has been properly aged and cured

TYPES AND VARIETIES OF TOBACCO

In India many commercial types of tobacco are grown These, based on their use, are flue cured or cigarette, bidi, cigar and cheroot, hookah, chewing and snuff, cigar wrapper, and other special purposes types Special varieties of *Nicotiana tabacum* (Fig 15 1A), the principal cultivated species, are grown for each of the different purposes Varieties of *N rustica* (Fig 15 1B), the other cultivated species of tobacco grown in India, are used for hookah, chewing, snuff, and sometimes in bidi, but are not suited for the other commercial uses *N rustica* is grown in the northern and northeastern region of India since it requires a cooler climate, while *N tabacum* is grown throughout the country About 90 percent of the total acreage in India is planted to *N tabacum* and 10 percent is planted to *N rustica*

Flue cured or Cigarette Tobacco. Flue-cured varieties have been derived mainly from what is known as Virginia tobacco, a type introduced from the U S A , but they also include some desi varieties locally known as natu [30] The bulk of the flue-cured tobacco is grown in Andhra Pradesh but some is also grown in Mysore, Maharashtra, and Gujarat The most widely grown varieties have been Harrison Special, Amerelo, Chatham, Hicks and Delcrest All are introductions, or selections from introduced populations, mostly from the U S A or Canada The flue cured tobacco constitutes the principal export tobacco from India [33 37] The leaf colour of the natu tobaccos varies from light brown to dark brown The light brown leaves are used for cheap cigarettes while the dark ones are used for pipe and shag tobacco The varieties of flue cured or cigarette tobacco belong to the species *N tabacum*.



15 1A

15 1B

Fig 15 1 Plants of tobacco A *Nicotiana tabacum* (flue-cured variety) B *Nicotiana rustica*.

Bidi Bidi tobacco is grown chiefly in Gujarat and Mysore states The principal varieties in Gujarat are Kelia Gandia Saijpuria and Pilia and the main varieties grown in Mysore are Surt 20 Nipani and Sawari All belong to the species *N tabacum* Pandharpuri a variety of *N rustica* is sometimes used to give strength to bidi mixtures [23]

Cigar and Cheroot Type Cigar and cheroot type tobacco is grown principally in Madras and West Bengal but some is also grown in Andhra Pradesh The Jati Bhengi variety of West Bengal is mainly used for making cheroots The main variety grown in Madras for making cheroots is Oosikappal The varieties grown in Madras for making cigars include Yerumaikappal Monnakappal Mandiyal and Adugumalli The main varieties grown in Andhra Pradesh for making cheroots are Lanka [32] Chebrole Baru Mentado Zarda Paira and Desi Nurvid All belong to the species *N tabacum* [23]

Hookah Type Assam West Bengal Bihar Uttar Pradesh and Punjab states grow most of the hookah tobacco Both *tabacum* and *rustica* varieties are used for hookah tobacco The hookah *tabacums* are called Des or Jati in Assam Jati in West Bengal Desi in Bihar [34] Poorbi in U P and Noki Kakka Ghora and Gidri in Punjab There are various varieties in each of these groups The main *rustica* varieties are Calcuttia Gobhi Motihari and Vilayat [35] Some varieties like N P 18 are grown in several states Tobaccos of Gujarat and Mysore are also used for hookah tobacco About 75 percent of tobacco of Punjab is *N rustica*

Chewing and Snuff Type Several bidi cheroot and hookah varieties are used also for chewing and

snuff Generally leaves with medium or thick texture and pungent aroma are used for these purposes In Bihar and Uttar Pradesh a variety, N P 70 has been developed for chewing tobacco only Both *N tabacum* and *N rustica* varieties are used for this purpose

Wrapper Type. A wrapper type tobacco variety, Rangpur Sumatra, is grown in West Bengal It is a selection from a variety introduced from Indonesia Another introduced variety, Dixie Shade, is also performing well [29] Possibility of growing wrapper tobacco at higher altitudes of 3500 to 4500 feet above sea level is being studied [31]

Other Types. An important *tabacum* variety, White Burley, is grown in Andhra Pradesh White Burley was introduced from the U S A and is used for blending in cigarette, pipe and chewing tobaccos Turkish is another *tabacum* variety with a distinct and mild aroma which is grown for blending with cigarette tobaccos

A list of commercial types and representative varieties grown in India are presented in Table 15 1 The varieties in cultivation change with the development of new varieties, so the student must consult his local agriculture department or agricultural extension service, or the agricultural university or college in his area for currently recommended varieties

BOTANY AND GENETICS OF TOBACCO

Tobacco is in the genus *Nicotiana*, a member of the *Solanaceae* or nightshade family This family includes the potato, tomato, pepper, eggplant, petunia and other food, ornamental, and medicinal plants, some of which are poisonous Sixty five species of *Nicotiana* are now recognized [1 15] Nearly one half of these species are indigenous in South America and the remainder in North America, Australia or the South Pacific Islands [15] There are two important cultivated species of *Nicotiana*, *N tabacum* and *N*

Table 15 1. Commercial Types and Varieties of Indian Tobacco[a]

Commercial type	*Area of production*	*Representative varieties*
Flue-cured	Andhra Pradesh, Mysore	Harrison Special, Harrison, Special 9, Chatham, Delcrest, Virginia Gold, Amarelo 5, Thokkaku, Desa Vali, Dakshinarthi
Bidi	Gujarat, Mysore	Kelin 49, Kelin 20, Gandin 6, Surti 20, Saij purin 57, Pilin 98, Ramol 43
Cigar and cheroot	Madras, West Bengal, Andhra Pradesh	Oosikappal, Monnakappal, Yerumaikappal, Mandival, Jati Bhengi, Lanka 27 (DR 1)
Hookah	Assam, West Bengal, Bihar, Uttar Pradesh, Punjab	Sindurkhatua, Kadamdal, Hatkania, Patuakhol, Barapat Bhengi, Mena Bhengi, Naokhol, Sindur Khots, Hingli, D P 401, N P 18, N P 219, N P 220, N P 222, T 23, T 59 Desi, Calcuttia, Gobhi, Vilayati
Chewing and snuff	Assam, West Bengal, Bihar, Uttar Pradesh, Punjab, Madras, Gujarat	Desi, Jati, N P 70, Oosikappal, Kali Chopadia, Judi, N P 219, N P 220, N P 222, D P 401
Wrapper	West Bengal	Rangpur Sumatra, Dixie Shade
Other types	Andhra Pradesh, Gujarat	White Burley, Turkish, Pandhar Puri

[a] *Indian Tobacco*,[23] Murty,[30] Murty *et al*,[32] Murty *et al*,[34] Randhawa [37]

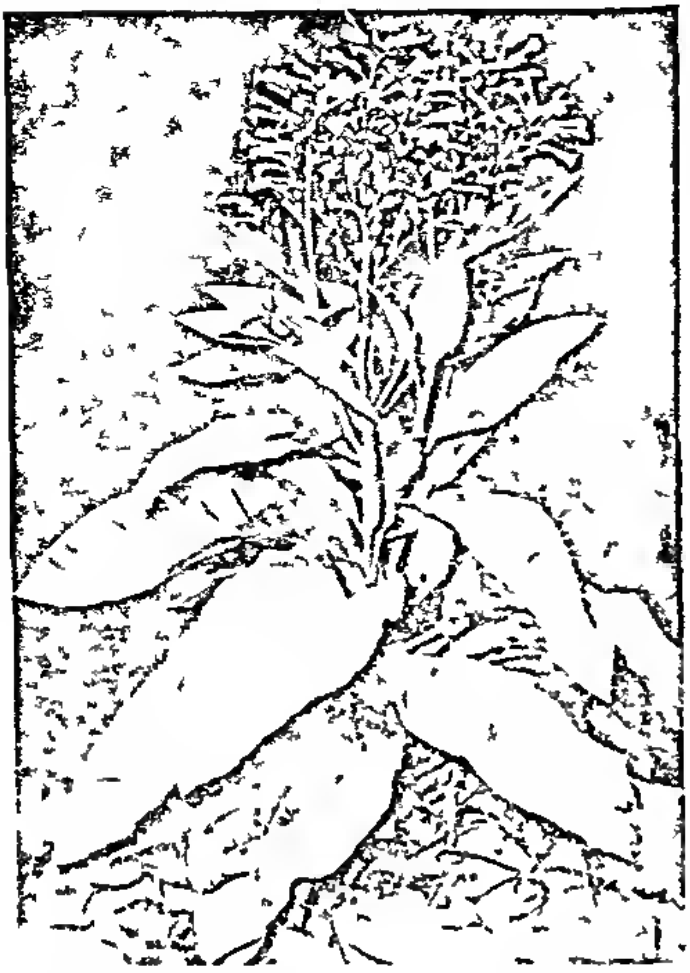


Fig 15 2 Inflorescence of tobacco a terminal raceme which bears many flowers The type shown here is Lanka an indigenous tobacco grown in the islands of the river Godavari

rustica Neither has been found growing wild *N tabacum* is grown and used most extensively for smoking and chewing tobacco although *N rustica* is also grown for hookah, chewing and snuff as already related

Haploid chromosome numbers of species in the genus *Nicotiana* range from 9 to 24, but the most common numbers are $n = 12$ and $n = 24$ [15] *N tabacum* and *N rustica* each have diploid chromosome numbers of $2n = 48$ *N tabacum* is believed to be an amphidiploid which originated by hybridization between *N sylvestris* ($n = 12$) and a species of the *Tomentosae* group probably *N otophora* ($n = 12$) [14 15 16] *N rustica* appears to be an amphidiploid which originated by hybridization between the species, *N paniculata* ($n = 12$) and *N undulata* ($n = 12$) [15]

The leaves of tobacco vary greatly in shape, texture, and number, depending upon the variety, the environment and the cultural practices Topping and suckering are generally practiced to promote growth of desirable leaves The ability to accumulate nicotine in the leaves is a characteristic feature of the tobacco plant Nicotine, an alkaloid having the formula $C_{10}H_{14}N_2$, is synthesized in the roots but is found in all plant parts except the mature seed and is stored most abundantly in the leaves [7 12] The amount of nicotine, and a related alkaloid, nornicotine, differ greatly in different varieties and species of *Nicotiana*

Flowering The inflorescence of tobacco is a terminal raceme which may bear as many as 150 flowers (Fig 15 2) [13] The corolla contains five petals which are fused into a long tube and which terminate in five expanded lobes at the top (Fig 15 3A) The petals are usually pink, although they may vary from white to red in certain varieties The flower bears five anthers, which are fused to the corolla tube (Fig 15 3B), and a pistil with a long slender style and a blunt two-lobed stigma (Fig 15 3C) The stigma is generally sticky and pollen adheres to it readily Tobacco is normally self pollinated, although as much as 4 to 10 per cent of cross pollination occurs from pollen carried by insects The extent of natural cross pollination is such that it is desirable to bag seed heads to ensure self pollination (Fig 15 4) [13] Flowers that are open or those already pollinated should be removed before bagging Dusting seed heads with an insecticide before bagging is desirable to prevent insects from feeding on the flowers inside the bags

The seeds of tobacco are extremely small and are usually borne in a two-valved capsule (Fig 15 3C, 15 5) A single flower may yield from 2,000 to 5,000 seeds and several hundred thousand seeds may be produced on a single plant of *tabacum* [13] Plants of *rustica* yield about one fourth this number of seeds

This tremendous capacity for seed production permits a rapid increase of new strains or varieties Tobacco seeds are long lived and if properly stored in a cool dry place may retain their viability for fifteen to twenty years

Artificial cross pollinations are easily made in tobacco if normal mature flowers are used All open flowers and seed pods are removed first, leaving only flowers that have not shed pollen The proper stage for emasculation may be identified by

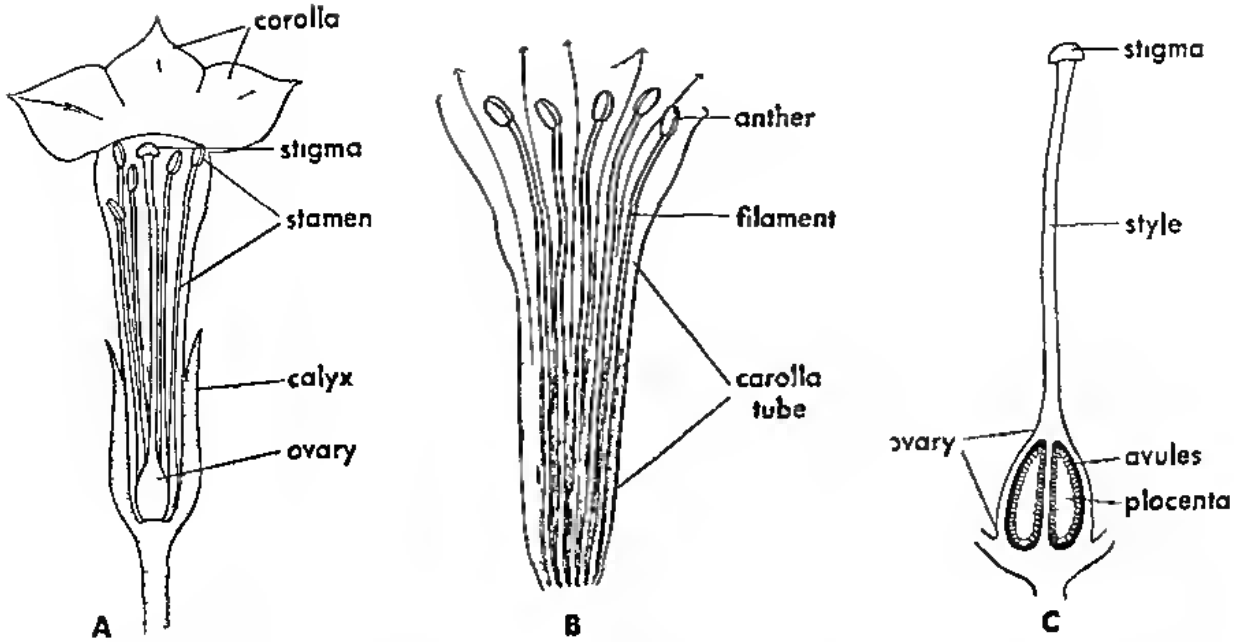


Fig 15 3 Flower of tobacco A Longitudinal section through flower showing the calyx corolla stamens and pistil B Section of corolla showing the five stamens with the lower portion of the filaments fused to the corolla tube C Pistil with longitudinal section of ovary showing two-valved capsule and fleshy placenta on which as many as 2 000 ovules are borne

Fig 15 4 Tobacco plant with seed head bagged to prevent natural cross pollination Although normally self pollinated the tobacco plant may be cross pollinated by insects which visit the flower to obtain nectar Flowers are bagged also following artificial crossing

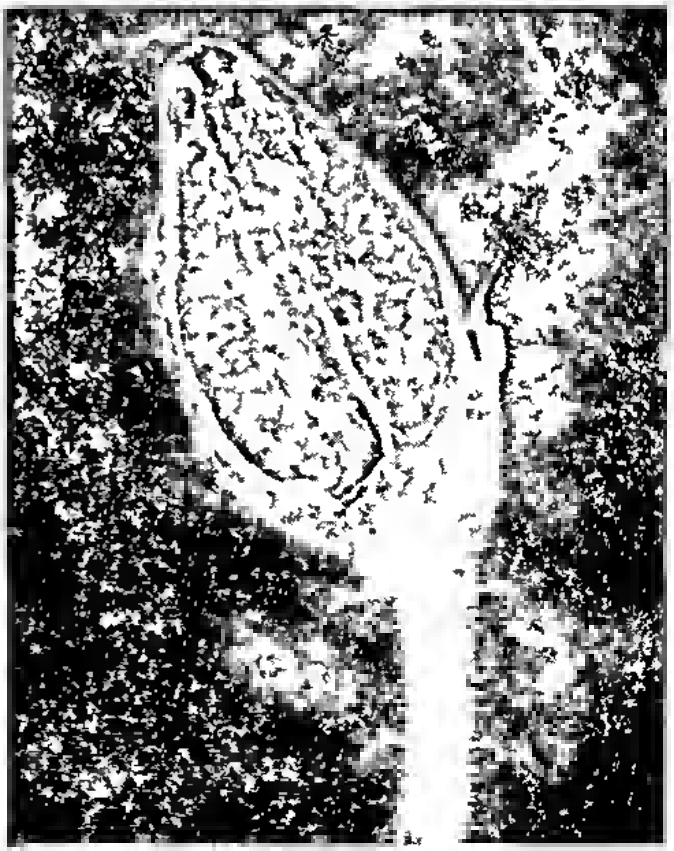
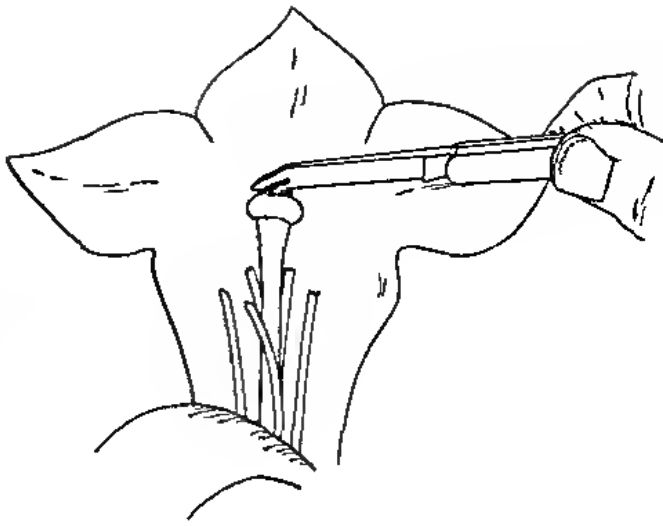


Fig 15 5 Longitudinal section through a seed pod of tobacco showing the two-valved capsule and many ovules A single flower of tobacco may yield 2 000 or more seeds

15 6A



15 6B

Fig 15 6 Crossing procedures in tobacco A Removing anthers with a pair of small tweezers B Pollen being transferred to the stigma of the emasculated flower on a knife blade

the presence of a pink colour in the tip of the petals of the unopened flowers The nearly mature flowers are emasculated by tearing the petals apart and plucking off the anthers either by hand or with small tweezers (Fig 15 6A) At the same time flowers from the pollen parent are selected which have fully developed anthers that have not opened With the point of a sharp knife a slit is made in the mature anther and a small amount of pollen is transferred to the stigma of the emasculated flower on the point of the knife blade (Fig 15 6B) After being pollinated the flowers are marked and then bagged to keep out stray pollen

Genetics Many genetic studies have been made with common tobacco (*N tabacum*) and other species of the genus *Nicotiana* Hybridization of tobacco was accomplished by the German hybridizer Koelreuter, as early as 1761 and by other early hybridizers long before the time of Mendel During the past forty years extensive studies of interspecific hybridization have been made by East,[8] Goodspeed [15] and others [22] Several reasons account for the vast genetic studies with the tobacco plant Tobacco is normally self pollinated but also easy to cross pollinate Large quantities of seeds are produced which remain viable for many years Common tobacco is extremely variable and furnishes many different plant characters to study Wide variations in characters are found in many closely related species which cross more or less readily with common tobacco

The extensive variability within the species *N tabacum* has afforded an opportunity to study the inheritance of a large number of characters such as flower colour and size internode length leaf shape and size leaf texture leaf base characteristics and number and size of suckers Some of these studies concern the practical breeder only indirectly but those dealing with flowering time disease resistance leaf characteristics, leaf quality nicotine content and similar characters are of agronomic importance and of direct interest to the breeder [28 49 50]

Interesting and valuable studies on the self and cross fertility relationships of plants of *N alata* and other *Nicotiana* species have been made by East and coworkers [8 9 10] Their experiments demonstrated that self and cross compatibility are dependent upon the rate of pollen tube growth In compatible matings pollen tube growth is rapid the pollen tube soon reaching the ovule where fertilization may be consummated In incompatible matings the pollen tube growth is very slow, and may not extend more than halfway down the style after ten days, which is generally the maximum life of the flower [8] The differences in rates of pollen tube

growth are controlled by a series of multiple alleles, S_1, S_2, S_3, etc (Fig 3 17) A pollen tube with an allele like that present in the mother plant grows very slowly A pollen tube with an allele different from that present in the mother plant grows at a normal rate In a study of failure in crosses of *N tabacum* × *N rustica* and *N tabacum* × *N debneyi*, it was observed that the longer length of the style in *N tabacum*, as compared to *N rustica* and *N debneyi*, leads to premature abortion of the pollen tubes [45] The reciprocal crosses were successful

Interspecific crosses have been made freely within the genus *Nicotiana* *N tabacum* ($n = 24$) has been crossed with *N alata* and *N langsdorffii* ($n = 9$), *N longiflora* ($n = 10$), *N glauca*, *N stylestris*, *N tomentosa*, and *N glutinosa* ($n = 12$), *N suaveolens* ($n = 16$), *N rustica* *N bigelovii*, and *N debneyi* ($n = 24$), and many others [8 14 15 25] Many of these interspecific crosses are of unusual interest to the breeder Crosses with *N. rustica* have been used in breeding for higher nicotine content and resistance to black shank Crosses with *N longiflora* have been used in America to obtain resistance to wildfire, a bacterial disease *N glutinosa* has been used as a source of resistance to mosaic Near immunity to black root rot has been transferred to common tobacco from *N debneyi* The technique used most successfully in transferring resistance genes from these species to common tobacco has been to double the chromosome number of the hybrid plant with the aid of colchicine and to backcross the amphidiploid to common tobacco [1] It is important that the character being added from the wild species is monogenic and dominant in inheritance so that plants exhibiting the desired character can be identified and selected from the progenies for further backcrossing Repeated backcrossing, selfing and selection are required until a chromosome segment containing the disease resistance gene is translocated into a *N tabacum* chromosome [1]

The polyploid nature of tobacco has stimulated many cytogenetic studies within the genus *Nicotiana* [38 40 41] By the use of colchicine, it has been possible to double the chromosome number in many species hybrids and obtain fertile amphidiploids In some cases the chromosome genomes from three species of *Nicotiana* have been combined by crossing amphidiploids with a third unrelated species.[25] Quadruple genome combinations (single genome from four species) have been produced in a similar manner In addition to the production of amphidiploids, autopolyploids have been produced in several species Autotetraploids produced by doubling the chromosomes in species with a low basic number, such as *N langsdorffii* ($n = 9$), have larger cells, thicker stems, broader leaves, larger flowers, and later maturing plants than the corresponding diploids [41 42] When the chromosomes are doubled again to produce octoploids, the plants are less vigorous When the chromosomes of *N tabacum* and *N rustica* are doubled, the induced polyploids are reduced in size although the leaves are thick have large stomata, and a dark green colour These results are explained by assuming *N tabacum* and *N rustica* ($n = 24$) to be tetraploids already and to have originated from the combined genomes of two species with chromosome numbers of $n = 12$ and when the chromosome number is again doubled the resulting plant is in reality an octoploid

METHODS OF BREEDING TOBACCO

The principal methods of breeding tobacco are introduction selection and hybridization Modern breeding work on tobacco was started about the beginning of the present century in the U S A, and other countries Through the efforts of the Dutch scientists breeding work on tobacco was initiated in Indonesia which led to the development of some excellent strains of cigar wrapper tobacco for that area Breeding of tobacco has been in progress in the Philippines for many years In India, improvement work on tobacco was initiated by the Howards at Pusa as early as 1906 [20 21] and later continued at the Indian Agricultural Research Institute Subsequently, breeding work was started in several states of India and, since partition, in Pakistan Tobacco processing and export companies were active in introducing and trying different foreign types from time to time However, no comprehensive and coordinated programme of improvement was started until after the formation of the Indian Central Tobacco Committee in 1947. Since then a number of tobacco research stations have been developed where breeding of the various types of tobacco grown in India is conducted [37] Some of these stations are as follows

- Central Tobacco Research Institute, Rajahmundry, Andhra Pradesh

Cigar and Cheroot Tobacco Research Station, Vedasandur, Madras State
Cigarette Tobacco Research Substation, Guntar, Andhra Pradesh
Hookah Tobacco Research Substation, Ferozepur, Punjab
Hookah and Chewing Tobacco Research Station, Pusa, Bihar
Bidi Tobacco Research Scheme, Anand, Gujarat
Bidi Tobacco Research Substation, Nipani, Mysore State
Wrapper and Hookah Tobacco Research Station, Dinhata, West Bengal

Unlike crops grown for their seeds the economic value of tobacco lies in the quantity and quality of the leaf Leaf quality in particular is very complex depending mainly on its chemical makeup which cannot be seen or measured easily

Introduction. Introduction has played an important role in the establishment of tobacco varieties in India Tobacco was first introduced into India by the Portuguese in the beginning of the 17th century [29] The crop soon spread into the different regions of the country and various local or desi varieties became established A large number of varieties from various countries, especially from the U S A, have been introduced and tried from time to time The flue cured varieties, Harrison Special and Hicks are introductions from the U S A The Delcrest variety of flue cured tobacco is an introduction from southern Rhodesia [33] The wrapper tobacco variety, Rangpur Sumatra, is a selection from an introduction from Indonesia Other important introductions include White Burley from the U S A and Amarelo from South Africa A genetic collection of nearly 500 strains being maintained at the Central Tobacco Research Institute contains introductions from many areas of the world

Selection. Pure line selection has been the main method of breeding in the establishment of most of the improved tobacco varieties in India Selections have been made from some introduced varieties, such as Harrison Special 9 from Harrison Special, and Chatham from an unselected cross made in Chatham, Virginia, U S A

The local tobaccos grown in India have a wide range of variability [24 28] The Lanka varieties, grown for many years on the Krishna and Godavari tracts, have been found to be quite variable genetically From collections of the latter area alone twenty distinct types have been established [32] The influence of environment is so great in tobacco that it was commonly believed that a variety could be induced to "break up" into many strains if moved into a new location, particularly from a semitropical to a temperate climate [44] It has been demonstrated, however, that much of this variation is due to segregation following natural cross pollination and that true breeding lines could be established by continuous bagging of flowering heads to protect them from foreign pollen [17 39] In selection for local materials, bulks of the local materials are collected and selfed for two or three generations after which distinct types can usually be isolated by pure line selection Improved varieties of all types of tobaccos in India have been established through selection procedures

Hybridization. As in other crops, hybridization became more important in breeding tobacco as knowledge of genetics increased, for, recombinations of plant characters could be obtained more or less to fit the breeder's design Large numbers of improved varieties have been developed by hybridization, principally in the U S A, in which were combined genes for larger number of leaves, improved quality, and disease resistance Hybridization has played a less important role in the development of new varieties in India but will become more important as present breeding programmes develop Hybridization of introduced flue cured varieties with local Indian varieties often led to poor curing characteristics in the leaves of the hybrid selections It is quite possible that this will be remedied as additional crosses using more diverse germ plasm are made Some synthetic strains have been built up in a multiple crossing programme involving superior varieties from many countries

A INTERSPECIFIC HYBRIDIZATION Interspecific hybridization has been an important procedure in the breeding for disease resistance in the U S A In many instances resistance genes for specific diseases could be found only in other species of *Nicotiana* [1] This necessitated the use of interspecific crosses as already described [3] With interspecific crosses, deleterious genes are often added to the adapted variety along with the genes for disease resistance To overcome these undesirable features and to recover

the plant type and quality characteristics of the adapted variety type, backcrossing to the common tobacco variety was practiced Backcrossing has been used also with intervarietal crosses, but the intensity of backcrossing is not generally as great as with interspecific crosses The large number of species of *Nicotiana* which have resistance to common destructive diseases of *tabacum* makes this a rich field for the breeder [1] In India, crosses involving *N glauca* have been made to transfer genes for powdery mildew resistance to *tabacum* [2]

B UTILIZATION OF HYBRID VIGOUR Numerous studies have been made on the expression of hybrid vigour in tobacco Hybrid seed production in tobacco does not present any problem as 2,000 seeds can be obtained from a single hand pollination About 300 flowers are sufficient to produce hybrid seed for one acre The emasculation process in tobacco may be eliminated by the utilization of cytoplasmic male sterility Cytoplasmic male sterile plants may be obtained by introduction of *tabacum* chromosomes into cytoplasm of *N debneyi*, *N megalosiphon*, and other species [27] By repeated backcrosses to male sterile plants varieties of *N tabacum* may be sterilized When the male sterile plants are supplied with fertile pollen, seed production is normal Restorer genes are not needed since it is the leaves of the F_1 plants that are harvested and seed production in the F_1 is unnecessary

Although hybrid vigour has been reported for early maturity, height, leaf number, and other characters, the increase in yield has not been encouraging In a comparison in North Carolina with variety crosses of flue cured tobaccos, 10 F_1 hybrids yielded about 4 percent above the average yield of the two parents [27] From these and other studies the commercial advantages of F_1 hybrids over available pure line varieties at present appear to be very slight Studies need to be made of yields with crosses of diverse germ plasms and also of quality and uniformity of hybrids as compared to standard varieties

Mutation Breeding. Use of irradiation or chemical mutagens for creating variability has already been demonstrated [23 36] Although creation of a large number of viable mutations is possible in tobacco due to its amphidiploid genotype, the quality requirements of the plant makes it difficult to obtain a desirable mutant directly Hybridization may be necessary to transfer the desirable mutant character to adapted varieties Progenies of each capsule should be advanced separately, following irradiation [36]

Polyploidy. Since cultivated tobacco is already a polyploid plant, achieving success by production of polyploids in tobacco may be difficult Polyploidy is useful in making interspecific crosses for the transfer of disease resistance or other desirable characters

OBJECTIVES IN BREEDING TOBACCO

Different quality characteristics are necessary for tobaccos used for different purposes This has necessitated development of breeding programmes for each of the various types of tobacco grown in India Nevertheless certain broad objectives may be stated which will apply to all classes of tobacco These include yield, field and handling characteristics disease and pest resistance, and quality Early maturity and frost resistance are important for tobacco grown in certain areas of north India

Yield. The yield of the tobacco plant is determined by number, size and body of the leaves Varieties of different types differ greatly in these characteristics, but yields of these different types are never compared directly since the types are grown in different areas and for different purposes In general yield has not been given first consideration by the tobacco breeder if it means a radical alteration in the characteristics of the variety already being grown The market in each production area has been established largely on the basis of the varieties already in production, and drastic variety changes are not favoured by growers or manufacturers of tobacco products Where yields have been reduced by a serious disease, attention may be centred on the breeding of disease resistant varieties as a means of preventing yield losses To receive general acceptance, the disease resistant varieties must produce satisfactory yields and have acceptable quality In evaluating tobacco varieties there is danger in relying too heavily on total yield per acre Consideration needs to be given also to the proportion of the respective grades of leaf tobacco produced on the plant Very little attention has been given to response to fertilizer in breeding varieties for high yield

Improved Field and Handling Characteristics. Various improvements may be made which will improve the field and handling characteristics

of tobacco These include such features as

1 Toughness, so that the leaves will stand rough handling

2 Storm resistance, to prevent breakage in wet weather when plants are turgid

3 Scald resistance, to reduce the wilting and killing of leaf areas on hot days

4 Uniformity of ripening to prevent lower leaves from falling off or deteriorating in quality before the upper leaves are ready to harvest

5 Stand up" types, which are easier to harvest and have less damage from leaves lying on the ground

6 Fewer suckers, small suckers, or slower growing suckers to reduce the labour cost of their removal

Curing properties of the leaf have received little attention but could probably be improved by breeding Curing properties are complicated by the fact that different varieties and types of tobacco have characteristics which respond differently to the various curing procedures

Disease Resistance. In many areas of the world major emphasis in breeding tobacco has been given to the breeding of disease resistant varieties Control of disease by chemicals where such disease control is possible, interferes with quality in many cases, hence development of disease resistant varieties offers the primary solution of the disease problem With some diseases in which practical control by chemicals is not available such as with root rotting organisms, breeding for resistance is necessary to maintain yield The important diseases of tobacco in south and southeast Asia are black shank, bacterial wilt, Fusarium wilt, powdery mildew, anthracnose mosaic, leaf curl, and nematodes [23 24]

Much progress in breeding for disease resistance in *N tabacum* has been made in the U S A [1] Some of the lessons learned from their experiences indicate that (*a*) Resistance to black shank and bacterial wilt is present in common tobacco (*b*) Adequate resistance to many diseases is found only in wild species of *Nicotiana* (*c*) Intraspecific resistance is frequently polygenic, although interspecific resistance is often simply inherited (*d*) Transfer of high resistance or immunity from other species usually results in the production of strains undesirable in plant type, yield or quality unless backcrosses are made to eliminate the undesirable genes introduced from the alien species (*e*) Desirable genes in other species are sometimes linked with undesirable genes For example, genes for nematode resistance are linked with genes for narrow leaf shape Since breeding work on disease resistance in tobacco in India is limited, examples will be cited of progress in the U S A with several diseases

A BLACK SHANK (*Phytophthora parasitica* var *nicotianae*) The black shank disease is characterized by blackened dead roots and the decay extends into the pith and cortex at the base of the stem (Fig 15 7A) [26 51] Infection later develops to the extent that the plants die (Fig 15 7B) The black shank disease was first identified in the U S A about 1916 Florida 301, a resistant shade tobacco variety was developed about 1930, by crossing and selection within local varieties of Big Cuba and Little Cuba [46] Florida 301 was later used as the source of resistance in the breeding of other black shank resistant varieties [4 5 50] Some of the black shank-resistant varieties developed in the U S A are RG, Oxford 1, 2, 3, and 4, Dixie Bright 101 and 244, Vesta, and Dixie Shade Resistance to black shank appears to be controlled by multiple factors and varieties differ in degree of resistance In the moderately resistant varieties seedling plants may be killed by invasion of the black shank fungus, but in older plants only a portion of the root system is damaged and the tobacco yield is not greatly reduced Some species of tobacco, *N longiflora* and *N plumbaginifolia*, are highly resistant or immune [5] Resistance genes from these species are being transferred to common tobacco

B BACTERIAL WILT (*Pseudomonas solanacearum*) Bacterial wilt was reported in the U S A more than fifty years ago It is a common disease in Sumatra, also, but is not so important in India Roots of diseased plants decay, and the plants wilt in a manner similar to those infected with the black shank disease (Fig 15 8) [26] Breeding work on resistance to bacterial wilt was started in 1934 by studying 1,034 collections of tobacco from Mexico, Central America, and South America [50] One plant was found to be highly resistant The strain developed from the plant T I 448A has been used as a source of resistance in breeding the variety Dixie Bright 244, which has resistance to black shank and Fusarium wilt as well as bacterial wilt Resistance to bacterial wilt is controlled by multiple recessive genes [43] Young plants are not as wilt resis-

15 7A 15 7B

Fig 15 7 A Black shank disease in a tobacco stem B Black shank susceptible variety (*centre*) with resistant flue-cured variety Oxford on either side

tant as adult plants Many plants in a wilt resistant variety may appear to be infected early however most recover with only slight ill effects [5] Resistance has not been found in other species of *Nicotiana* Resistant lines have been developed in Sumatra [24]

C FUSARIUM WILT (*Fusarium oxysporum* var *nicotianae*) Fusarium wilt is an important disease in India Tobacco plants infected with the Fusarium wilt turn yellow on one side of the plant because of the production of toxin by the Fusarium organism After the tissue is broken down the plant wilts [26] Many flue cured varieties grown in the U S A are resistant Resistance to Fusarium wilt is inherited by a single factor pair [50] Artificial inoculations to test for resistance may be made at the time plants are set in the field by dipping the plants into solutions carrying the wilt producing organism

D POWDERY MILDEW Powdery mildew (*Erysiphe cichoracearum* var *nicotianae*) is an important disease in India Mauritius East Indies and the Philippines The infection spreads rapidly in the field destroying the crop The affected leaves develop defects on curing or even get scorched rendering them useless for marketing Immunity has been transferred to *N tabacum* varieties from *N glutinosa* and other species [1] Selections from these crosses are being used as sources of resistance in the East Indies [24] Crosses to transfer resistance of *N glauca* to *tabacum* have been made in India [2] (Fig 15 9)

E ANTHRACNOSE Anthracnose (*Colletotrichum tabacum*) is a serious disease in tobacco nurseries in India Several wild species including *N debneyi* and *N longiflora* are reported to be resistant [1] Resistance in *N debneyi* is stated to be controlled by polygenic recessive genes [52]

F MOSAIC Mosaic caused by the tobacco mosaic virus is recognized by the presence of leaves with a conspicuous dark green and yellow green mottling which later may become puckered and deformed [26 51] The greatest mottling is usually found on the younger leaves Tobacco mosaic may be transmitted to healthy plants merely by rubbing first a diseased and then a healthy plant or by handling dried infected tobacco used for smoking or chewing and then handling living plants As a result the grower frequently spreads the disease in the field while handling his tobacco plants Mosaic infected plants are reduced in yield and quality with losses

Fig 15 8 Bacterial wilt susceptible variety Gold Dollar (*centre*) with wilt resistant varieties on either side On the left is T I 448 the original wilt resistant strain

Fig 15 9 Testing for resistance to powdery mildew Tobacco plants are grown under a hessian covering at the Central Tobacco Research Institute Rajahmundry India to keep the temperature and humidity favourable for the growth and spread of the powdery mildew organism

ranging up to 60 percent depending on how early in the life of the plant the disease is contracted Sanitation and use of disease resistant varieties are the only known means of control

Resistance to tobacco mosaic has been observed in *N glutinosa* ($n = 12$) and other species [1 50 51] The resistance of *N glutinosa* to mosaic was observed in 1916 by H A Allard[5] and was transferred later by Holmes to common tobacco [18 19] Resistance from *N glutinosa* was used in producing resistant commercial varieties in the U S A [47 48 50] Mosaic resistance from *N glutinosa* is inherited as a monogenic dominant character, one of the few tobacco diseases known to be inherited in so simple a manner [6] In resistant plants normally, leaf tissue is killed only in areas where the virus enters, and the virus is localized in these spots However, if parenchyma tissue such as midvein or cortex is infected the virus is likely to spread and kill the plant

G NEMATODES Several species of nematodes cause injury to tobacco The root knot nematode (*Meloidogyne* sp) is the most important one The root knot nematode causes the infected roots to become enlarged and knotted As the roots decay, growth of the plant is retarded and the leaves are killed prematurely Moderate resistance is found in the flue cured varieties 400 and 401 in the U S A and high resistance in the Central American variety T I 706 [50] Resistance of *T I 706* is polygenic Most highly resistant selections from crosses with T I 706 have had small leaf size Excellent resistance to root knot is found in *N repanda, N megalosiphon* and other species [1 5]

H OTHER DISEASES Other diseases that call for urgent attention in tobacco growing areas in south and southeast Asia are the frog eye leaf spot (*Cercospora nicotianae*) and the leaf curl disease Not much information about sources of resistance is available [1 52]

Quality Quality in tobacco is a complex characteristic which cannot be defined easily Quality varies with the kind and variety of tobacco the environment in which it is grown, the process employed in aging and curing the leaf, and the specific use of the tobacco Quality cannot be measured with finality by simple mechanical or chemical means, it depends upon the desires of the manufacturer and the taste of the consumer (Fig 15 10) The tobacco breeder has done little to improve quality His main concern has been to maintain the quality characteristics of the best tobacco types with which he is working As genes for disease resistance have been brought into the common tobacco chromosome complex from other species of *Nicotiana* it has become increasingly important to test a new variety for quality before it is distributed Many of the species used as sources of disease resistance genes have few, if any, of the elements of quality desired in *N tabacum*, so far as is known Backcrossing to common tobacco to eliminate undesirable genes from alien species is resorted to in order to maintain satisfactory quality, as well as yield and plant type Some of the components of quality that may be given consideration by the breeder are leaf characteristics burning qualities aroma and taste, sugar content and nicotine content Manufacturers are giving greater attention to chemical composition of the leaf than they did in the past

A LEAF CHARACTERISTICS The size shape colour, thickness and body of the leaf are characteristics affecting quality which vary with the variety, although they are also modified by the environment cultural methods and position of the leaf on the stalk It is more important that tobacco used in the manufacturing of cigars conform to specific requirements than tobaccos used for other purposes For cigar wrapper tobacco, types with short, thin

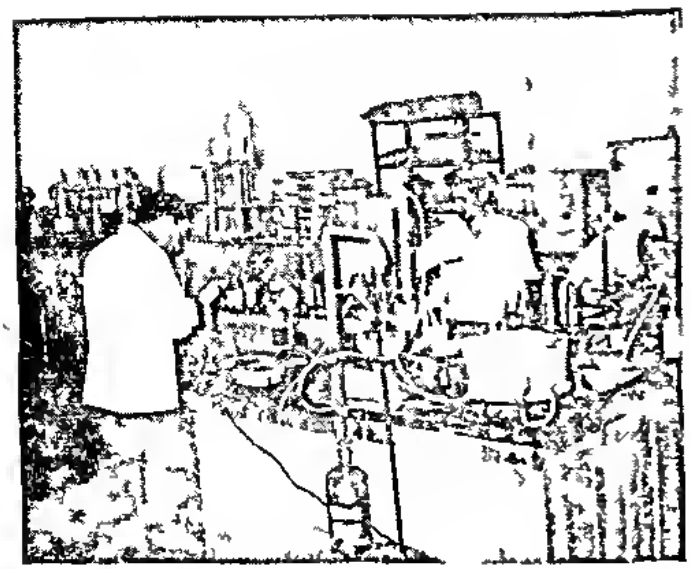


Fig 15 10 Tobacco quality testing laboratory at the Central Tobacco Research Institute Rajahmundry

leaves with less branched veins fine texture, and elasticity are preferred Thin leaves are also preferred for pipe smoking blends, thicker leaves for cigarettes, and the thickest leaf type of chewing tobacco [12] Wide leaves are desirable in any variety to give a high stripping yield

B BURNING QUALITIES, AROMA The burning quality, or combustibility, is an important consideration in quality of tobacco used for smoking This characteristic is determined by (*a*) the fire holding properties, (*b*) the rate, evenness, and completeness of the burn, and (*c*) the character of the residual ash [12] Burning qualities are affected by physical and chemical characteristics of the leaf, which vary with different varieties and soils Aroma is developed with the process of curing and aging, but varies with the variety Taste or flavour is important in the final product, but it is a difficult characteristic to evaluate

C NICOTINE CONTENT Interest in breeding low-nicotine varieties of cigarette tobacco has been stimulated by the desire to develop a variety which could be smoked without harmful effects High nicotine content is preferred in bidi, hookah and chewing tobacco It has long been known that the nicotine content is influenced by (*a*) the variety, (*b*) the environment in which the tobacco is grown, and (*c*) the cultural practices used in its production (Fig 15) [5 11] Heavy fertilization with nitrogen to increase yields, topping or suckering, and other practices often result in excessive percentages of nicotine

The nicotine contents of various Indian tobaccos are as follows cigarette type, 1 to 2 percent, cigar leaf, 2 to 3 percent, bidi, 6 to 8 percent, cheroot 3 to 4 7 percent, hookah, 0 5 to 1 5 percent in *tabacum* varieties and 2 to 3 5 percent in *rustica* varieties, snuff 3 2 to 4 8 percent [23]

There appears to be some dominance in inheritance of high nicotine content over low nicotine The F_1 of crosses between low nicotine and Burley strains in the U S A was high in nicotine, but in the F_2 the strains ranged from 0 to 2 82 percent nicotine Factors which control total alkaloid production (nicotine and nornicotine) are different from the factors which effect the conversion of nicotine to nornicotine or other products [49]

D SUGAR CONTENT Some emphasis has been given to breeding for higher sugar content in the flue cured tobacco leaf With the increased use of the cigarette, tobacco companies have been seeking mild thin leaf tobaccos lower in nicotine and higher in sugar Most flue cured varieties in the U S A average around 18 percent sugar, but it would be desirable if the sugar content could be increased to about 20 percent

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16

Breeding Pulses

The pulses include species belonging to the family *Leguminosae* which are cultivated for their edible seeds Those grown most extensively in south and southeast Asia are gram, bengalgram, or chickpea (*Cicer arietinum*), pigeonpea (*Cajanus cajan*), blackgram or mash (*Phaseolus mungo*), greengram or mung (*Phaseolus aureus*), lentil (*Lens esculenta*), horsegram (*Dolichos biflorus*), fieldbean (*Dolichos lablab*), kesary (*Lathyrus sativus*) and a few others The first six are of primary importance (Fig 16 1) Because they are high in protein content, the pulses provide a major source of protein in the diets of many people in this part of the world A few of the pulses, like gram, blackgram, and horsegram, are also used as feed for cattle Some of the pulses, particularly pigeonpea, gram and lentil, are grown in other parts of Asia, Africa, Europe, and the Americas In India, pulses occupy about twenty five million hectares with a total annual production of around 9 to 12 million metric tonnes (Table 16 1) Gram or chickpea occupies more than 40 per cent of the total area planted to pulses in India

Very little attention has been given to production or utilization of the soybean (*Glycine max*) as a pulse crop in India or Pakistan, even though it is widely used as a food crop in China, Japan and other countries The high nutritive value of the soybean (40 percent protein and 20 percent oil) makes it seem desirable that edible varieties of this species be developed for south and southeast Asia and ways found to process and cook them so that they will be palatable and acceptable to the people

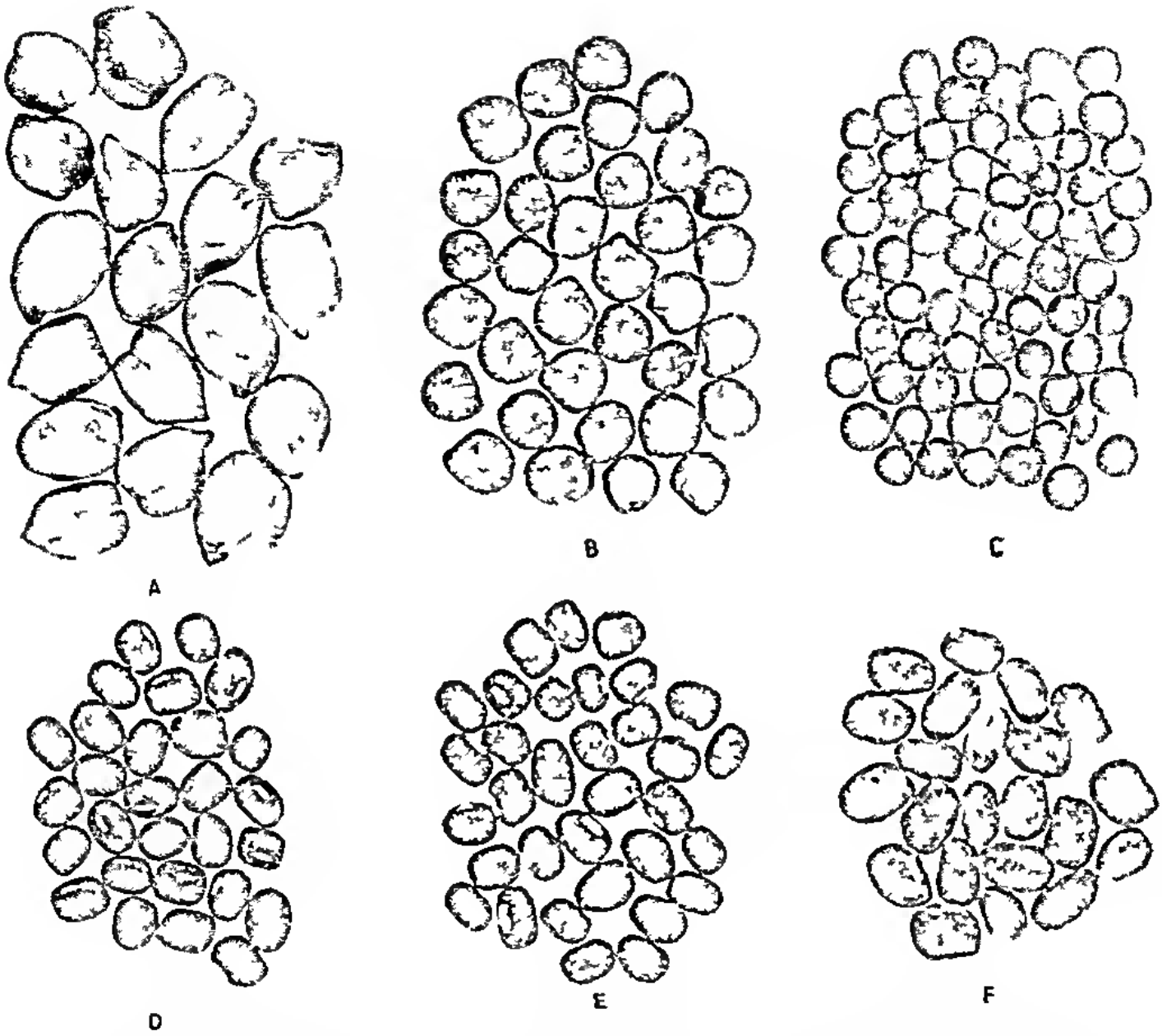
Table 16.1 Comparisons of Acreage and Production of Pulses in India

Crop name	*Area in million hectares*	*Production in million metric tonnes*
gram or chickpea	10 0	6 75
pigeonpea or arhar	2 5	1 64
horsegram	1 8	0 39
blackgram or mash	1 5	0 44
green gram or mung	1 4	0 30
lentil	0 7	0 24
others	6 5	2 74
Total	24 4	12 50

ORIGIN AND CLASSIFICATION

South and southeastern Asia is supposed to be the centre of origin of pigeonpea, blackgram, green gram, and probably *Dolichos*, while the eastern Mediterranean is the centre of origin of gram or chickpea (*Cicer arietinum*) and lentil [7,34]

Gram (*Cicer arietinum*) has been classified into as many as 84 types based on the persistent or deciduous character of the standard petal, colour of flowers, seed size, colour of grain, pod size, number of flowers on the peduncle, and other characters [22 45] It has also been suggested that the white grained, bold seeded 'Kabuli' gram should be a separate species of *Cicer* [18 19] Pigeonpea (*Cajanus cajan*) has been divided into two groups based on height, maturity, character of the standard petal and number of seeds per pod [34] The late maturing type, *Cajanus cajan* var bicolour, is the tallest of the two types and has flowers grouped at the end of the branches It contains 4 5 seeds per pod The other type, *Cajanus cajan* var flavus, is shorter, earlier maturing with flowers borne at several points along the branches, and bears 2 3 seeds per pod Blackgram (*Phaseolus mungo*) has been divided into two subspecies, niger and viridis [12] Plants of the first



F g 16 1 Seeds of some pulse crops mportant in south and southeast As a A Gram bengalgram or chickpea *Cicer arietinum* B P geonpea or arhar *Cajanus cajan* C Lentil *Lens esculenta* D Greengram or mung *Phaseolus aureus* E Black gram or mash *Phaseolus mungo* F Horsegram *Dolichos biflorus* (Seeds in photo are slghly reduced from natural size)

group are early in maturity and possess large, black seeds while those of the latter group are late maturing with small greenish seeds Based on the colour of flowers pods and seeds greengram (*P aureus*) has been classified into 40 types [11] The lentils are broadly divided into two subclasses macrosperma with large seeds and microsperma with small seeds Each subclass has been further divided based on such characters as size of flowers pods, and seeds and shape of pods

BOTANY AND CENETIC STUDIES

All of the pulses have typical papilionaceous flowers consisting of five sepals five petals comprised of one standard two wings and two keels, ten stamens nine fused to form a staminal column and one free and a carpel with the style borne laterally on the ovary (Fig 2 2 C and D)

In gram or chickpea (*Cicer arietinum*) anthesis starts between 9 and 10 A.M. and may continue up to 3 P M The flowers remain open for two days

the flowering process being over early on the second day The plant is primarily self pollinated as anthers dehisce about forty hours prior to opening of flowers A very small percentage of cross pollination may result from insect visitation after the flowers open Cleistogamy has also been recorded in the species [8 14]

The flowers of pigeonpea (*Cajanus cajan*) normally open during the early morning and remain open for about 36 48 hours Fertilization frequently occurs prior to complete opening of the flowers [33] In Hawaii less than 1 percent natural cross pollination was reported [25] but in India cross pollination up to 25 percent has been recorded [16]

In blackgram (*Phaseolus mungo*) and greengram (*P aureus*) the flowers begin to open between 6 and 7 A M and the flowering process continues for an hour or two They remain fully open until noon and then gradually close being completely closed by 2 to 4 P M [11 12] Pollination occurs in the bud stage and the anthers dehisce between 9 P M and 3 A M The petals are shed the following morning As anthers dehisce long before the flowers open self pollination is the rule Cleistogamy is prevalent to a great extent [14] Lentil (*Lens esculenta*) is essentially self pollinated although natural cross pollination may occur through insects

Diploid chromosome numbers of the principal cultivated pulses are listed in Table 16 2

Table 16 2 Diploid Chromosome Numbers in Some Species of Pulses

Crop name	*Species*	*Diploid chromosome number*[a]
gram or chickpea	*Cicer arietinum*	$2n = 14, 16$
pigeonpea	*Cajanus cajan*	$2n = 22, 44, 66$
blackgram	*Phaseolus mungo*	$2n = 22, 24$
greengram	*Phaseolus aureus*	$2n = 22, 24$
lentil	*Lens esculenta*	$2n = 14$
horsegram	*Dolichos biflorus*	$2n = 24$
fieldbean	*Dolichos lablab*	$2n = 22, 24$
kesary	*Lathyrus sativus*	$2n = 14$

[a] From Darlington[16] and Dixit[19]

Emasculation and Pollination. Flowers are generally emasculated in the evening and pollinated the next morning [14 25] For emasculation flowers that will open one or two days later are selected, and the rest of the flowers and buds in a branch are removed The stamens of the selected buds are removed with a pair of fine forceps by gently pushing the keels apart The emasculated floral branch is then bagged Utmost care is necessary in emasculation as the flowers in some species as in blackgram for example are very sensitive and may shed after emasculation or even after pollination Magnifying glasses may be needed in emasculating very small flower buds Ripe anthers are collected the following morning and pollination is done by gently pressing a ripe anther against the stigma The flowers are again bagged after pollination until the pods are mature

To ensure selfing the flowers need to be bagged, also, as insects may sometimes carry pollen to the stigma and bring about cross pollination In most breeding studies the amount of natural cross pollination is so small that it may be ignored

Genetic Studies. As pulses are widely grown in India numerous genetic studies have been made on these crops Many of the studies are related to flower colour, pigmentation of plant parts, tapering of the fruit tip, pod colour and others [3 6 13 37 40 41] Many of these genetic studies do not have much utility to the plant breeder There have been very few studies of inheritance of economic characters useful in breeding

Erect and semispreading habit of greengram is controlled by a single gene, spreading habit being dominant Twining and nontwining habits are also governed by one gene, the latter habit being dominant [21] Single podded is dominant to double podded and controlled by a single gene pair [2] Attempts have been made to improve yield by introducing the double podded character

METHODS OF BREEDING PULSES

Breeding methods used with the pulses are those that are normally followed in self pollinated crops These are introduction, selection, and hybridization In addition special techniques like irradiation and polyploidy may be used to increase genetic variability

Introduction and Germ Plasm Collections. The first step in any improvement work is to assem

ble germ plasm collections of indigenous and introduced varieties to be used as sources of breeding materials Introduced varieties may be used for direct growing, as sources of germ plasm for further selection, or for utilization in a hybridization programme Few, if any, varieties of pulses introduced into India have been grown commercially Shining Mung No 1, a variety of greengram, was developed by selection in Punjab from a Chinese variety [48] A bold seeded, white grained, African gram variety, Rabat, was crossed in Punjab with a local variety, Pb 7, to develop the white, bold seeded, improved variety C 104[5] (Fig 16 1A) Many introductions have been assembled at the Indian Agricultural Research Institute by the Plant Introduction Division and are available to pulse breeders in India as parent materials Plants of gram and fieldbeans are shown in Figs 16 2 and 16 3

Selection. Pure line selection from indigenous materials has been the principal method so far for improvement in pulses Since many of the pulses are indigenous to India and have been grown here

Fig 16 2 Plant of gram or chickpea, *Cicer arietinum* variety I C 8120 Seeds of this particular variety do not turn yellow or brown when they mature but retain a green colour characteristic of unripe seeds

Fig 16 3 Plants of fieldbean *Dolichos biflorus* growing in *Madras state*

for thousands of years, considerable variability exists within most desi varieties Pure line selection from local strains has been used extensively to develop varieties from local types in the different states of India [26 32 38 43 49] The variety of gram, G 24, a pure line selection from a local type, released in Punjab in 1958 has higher yield, drought resistance, early maturity, and wilt resistance [5] A drought resistant strain of pigeonpea SA 1, was developed in Madras state as a result of pure line selection [49] Improvements in the pulse crop by pure line selection for the most part have come about very slowly

Hybridization. Hybridization has been used to develop improved varieties only during recent years The wide variability present among the existing varieties in the different areas suggests good possibility for improvement of the crop by this method The gram variety, C 1234 was developed in Punjab as a result of a cross between Pb 7 and an exotic type, F 8 Better evaluation of the existing varieties is necessary in order to choose the best parental combinations Hybrid vigour, as expressed by higher yield of the F_1 over the best parent, has been noted in a few cases [35] However, no practical means of utilizing hybrid vigour in the self-pollinated pulses is available The backcross may be used to add specific genes for desirable characters to an adapted variety

Irradiation Breeding. Most of the mutation studies in pulses are confined to gram or chickpea Gram (*Cicer arietinum*) is claimed to be a more mutable crop than most other economic crop

plants [46] Many natural mutations have been reported also [19,20 30,46] These relate primarily to leaflet number, leaflet shape and size, foliage colour, seed fertility, pod shape and size, and growth habit Most mutants have been simple recessives to the normal [21 30 50] Mutations have also been induced in *Cicer*, *Cajanus*, and *Phaseolus* by irradiation [1 4,23] An early mutant of black gram (*Phaseolus mungo*) has been obtained from irradiated materials in Madras [49]

Use of Polyploidy. Polyploidy has been induced in the pulses by use of colchicine [21 39] In gram, treatment of germinating seeds with 0 25 percent solution of colchicine for 1/2 hour gave the best result The polyploids had gigas characters, flowered 4 to 5 days later than normal plants, and had 40 to 80 percent sterile pollen grains as compared to 10 percent in the normal In blackgram the polyploids had shorter pods and larger and heavier seeds They were less vigorous in growth and flowered over a longer period The pollen fertility was lower than the fertility in normal diploids Selection alone was not sufficient to overcome the reduced seed setting in greengram [42]

Pulse Improvement Research. A cooperative pulse improvement project has been initiated recently by the United States, Iran and India The initial research centre was established at Tehran-Karaj, Iran, in 1964 with a second research centre at New Delhi, India, in cooperation with the Indian Agricultural Research Institute Chickpeas, pigeonpeas, mungbeans, urdbeans, and related species will receive attention in India Research objectives include among others (*a*) the collection and assembly of germ plasm of the pulse species, (*b*) the breeding of improved varieties, (*c*) the coordination of regional testing programmes, and (*d*) the development of a seed multiplication system It is expected that this cooperative effort will be extended to include cooperation with many countries in the Near East, South Asia, and Far East regions

OBJECTIVES IN BREEDING PULSES

The main objectives in breeding pulses are yield, regional adaptability, suitable plant type, shattering resistance, disease resistance, insect resistance, and quality

Breeding for High Yield. The yield of the pulse crops is at present very low and there is great scope for its improvement by well planned breeding programmes The expression of yield in any particular genotype is affected by soil, climatic conditions, diseases, and pests Hence, proper attention has to be given to breeding not only for factors affecting yield directly, but also to screening for adaptation, disease resistance and other characteristics affecting yield Little is known regarding the response of different species or varieties to heavy fertilization

Regional Adaptability. Pulses are grown in every state in India and in other countries of south and southeast Asia For the most part pulses are short duration crops grown under rainfed conditions, often in low rainfall periods, although some may be grown under irrigated conditions They are grown on a wide variety of soils, from light sandy or gravelly soils to heavy clay Gram, lentils, and kesary are generally grown as cool season or rabi crops, while pigeonpea, greengram, and blackgram are warm season crops and are usually grown as kharif or autumn crops [34] Very little study has been given to what constitutes adaptation of a variety in the different agroclimatic regions Maturity, photoperiodic response, and drought resistance are physiologic factors affecting adaptation Most improvement in pulses has been limited to selection for local conditions without basic consideration of the requirements for adaptation in the particular area (Fig 16 4) With only local emphasis on improvement no attempt has been made to develop varieties for broad geographic areas in which varieties with similar adaptive characteristics may be grown Neither has there been any effort to develop strains responsive to high fertility In Punjab, cultivation of pulses in rainfed and low rainfall areas has led to development of drought resistant types For example, in Punjab the variety S 26 is recommended for rainfed areas while the variety S 33 has been developed for irrigated or adequate rainfall areas In blackgram, the variety Kulu Mash 4 is recommended for the hilly and submountain tracts In Madras the pigeonpea variety SA 1 is reported to be drought resistant Varieties to be grown in humid areas require resistance to blight and to root and stem rot diseases

Plant Type. The growth habit of the different pulses are different The gram, blackgram and greengram plants may be erect or spreading The branching behaviour also varies Generally, erect

Fig 16 4 Testing strains of pulse crops at the Madras Agricultural College and Research Institute Coimbatore

types which branch profusely which do not lodge and which hold the seed pods up off the ground are desirable for irrigated areas while the spreading type is suited to the rainfed areas as they shade the ground and help to conserve moisture in the soil In pigeonpea a perennial plant with good productivity may be useful

Breeding for Shattering Resistance The ripening pods in certain varieties tend to dehisce and release the seeds If the varieties shatter in the field a loss of yield will occur Varieties differ in their shattering habits and varieties that will not shatter after maturity are desired

Disease Resistance Breeding for disease resistance in pulses has been confined mostly to the blight and wilt diseases of gram and the wilt disease of pigeonpea

Gram blight is caused by *Phyllosticta rabiei* (Pass) Trotter [28] Studies on blight resistanee have been made in India and other countries and sources of resistance are available There is no adequate information regarding the races of the fungus available although in India there are indications of the occurrence of new races In Punjab the variety C 1234 which was originally found to be blight resistant was susceptible in later years The variety C 235 also is reported to be resistant to blight [10]

Wilt of gram is caused by *Rhizoctonia bataticola* A Fusarium wilt disease has also been reported The inheritance of Fusarium wilt resistance is reported to be controlled by a single pair of genes [9] but this seems much simpler than inheritance of resistance to Fusarium in other crops The variety C 24 from Punjab is reported to be resistant to wilt. In Pakistan the gram variety C 612 is reported to be resistant to blight and tolerant to wilt [47]

The most important disease of pigeonpea is wilt caused by *Fusarium udum* Butl Resistance is reported in the types N P 41 N P 51 and N P 80 [47] Crosses of N P 51 × N P 24 has resulted in the development of four highly wilt resistant selections N P (W R)15 N P (W R)16 N P (W R)19 and N P (W R)38 [17 36] The wild varieties *Atylosia lineata* and *A sericea* a genus related to *Cajanus* are reported to be sources of wilt resistance and have been utilized in crosses for this purpose [47] Resistance to wilt is stated to be controlled by a pair of duplicate dominant genes [24] and also by multiple genes [29 44]

The important diseases of blackgram and green gram include leaf spot incited by *Cercospora cruenta* and chlorosis The blackgram variety Kulu Mash 4 is reported to be resistant to leaf spot and the greengram selections 24 2 and 24 3 are resistant to chlorosis in Punjab

Insect Resistanee Although the pulses are infested by several insect pests little or no breeding for insect resistance has been initiated Identification of major insect pests and information regarding sources of resistance are needed for developing a programme of breeding for resistance in each of the pulse crops

Breeding for Quality Quality in pulse is determined by grain size colour cooking quality and nutritive value

In gram bold seeded white Kabuli types are preferred to the small seeded brown types The variety C 104 has been developed from a cross of Pb 7 with Rabat in Punjab Pb 7 is a small seeded gram with brown seed colour while Rabat is a bold seeded white low yielding Kabuli type from Africa The variety C 104 is white bold seeded and equal to Pb 7 in yield Green colour is preferred in some areas for culinary purposes [38] Lentils and pigeonpeas with large seed size also bring premium prices in the market

Little information is available on what constitutes good cooking quality Cooking quality is related to hardness of the grain Some pulses such as certain varieties of lentil tend to have hard seeds which do not cook well Since pulses are used mainly as a source of protein in the diet breeding varieties with high protein content and particularly for a high content of the more essential amino acids, such as lysine, would improve their nutritive

value as food Analyses of gram varieties has indicated that Kabuli types contain higher amounts of protein than the common types [27] Information on other pulses is very scanty in this respect No information is available on the kinds of proteins in the different varieties of the different species

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17

Breeding Oilseeds

Oilseed crops include a wide array of plants the seeds of which are used primarily for extraction of oil The important oilseed crops grown in south and southeast Asia include groundnut (*Arachis hypogaea*), rape and mustard (*Brassica sp*), sesame (*Sesamum indicum*), linseed (*Linum usitatissimum*), safflower (*Carthamus tinctorius*), castor (*Ricinus communis*) and niger (*Guizotia abyssinica*) The coconut (*Cocos nucifera*) is another important source of oil but it will not be discussed here The relative area planted to the different oilseed crops in India is shown in Table 17 1 The oil of the various crops is utilized for widely different purposes from cooking media to varnishes, lubricants, hair oil or medicine From the breeding standpoint, the oilseed crops comprise a heterogeneous group of species with varying modes of pollination and breeding behaviour For this reason each must be considered separately In addition to those named above, the soybean (*Glycine max*), because it has a high potential for oil production, will also be discussed even though present acreage is relatively meagre

BREEDING GROUNDNUT (PEANUTS)

Groundnuts are indigenous to Brazil in South America and from there were introduced into southeastern Asia, Africa and the U.S A. During the past one half century groundnut acreage has expanded and groundnuts have become an important food crop in many regions of the world India grows more than 6 million hectares and harvests about 60 percent of the total world production [19] Other countries growing large acreages include China, U S A , Senegal and Nigeria in Africa, and Burma, Malayasia, Pakistan and Ceylon in south and southeast Asia In India Andhra Pradesh, Maharashtra, Gujarat, and Madras states have the largest acreages although important acreages are grown also in Madhya Pradesh, Uttar Pradesh, and Mysore While used primarily as an oilseed crop in India, large quantities of groundnut are consumed directly as food The groundnut plant is used as a fodder crop and the oil cake as feed for cattle or for manure

Table 17.1. Areas Planted to Some Oilseed Crops in India

Crop	*Area in thousand hectares 1964/65*[a]
Groundnut	6,809
Rapeseed Mustard	3,023
Sesame	2,395
Linseed	2,006
Safflower	526[b]
Castor	477
Niger	324[b]

[a] From Ministry of Food and Agriculture, Government of India

[b] Estimates only

Botany. The groundnut (*Arachis hypogaea*) belongs to the *Leguminosae* family The plants are low growing annuals and the cultivated varieties vary in growth habit, plant type and seed characteristics The cultivated groundnuts may be divided into two distinct types, erect or spreading, and the seed is described on the basis of size as small, medium or bold [15] In the U S A the large or bold seeded varieties are referred to as Virginia peanuts and the small seeded types as Spanish A third type, "runner ', is also recognized Twelve species of *Arachis* have been described [10] but recent collections indicate that there may be as many as 30 to 50 species

The most striking characteristic of the groundnut plant is its manner of flowering and seed formation [10 23] The flowers are borne in the axils of the

leaves, mostly near the base of the plant, although the flowers may sometimes be borne below the ground level The flowers have yellow petals Eight to ten stamens form a monadelphous bundle but commonly only eight stamens bear anthers The stalk of the ovary elongates, forming what is known as the peg, and curves downward after fertilization pushing the ovary below the ground where the pods containing the nuts develop (Fig 17 1)

Groundnut is essentially a self pollinated crop, the extent of natural cross pollination being very small [13] The groundnut flower normally opens between 6 and 8 A M and the anthers dehisce about one to two hours before the flowers open Artificial crossing is tedious and time consuming Emasculation is done in the late afternoon or evening Flower buds that will open the next morning are selected for emasculation The petals are spread apart with forceps in order to remove the stamens, after which the petals are placed back in their original position Bagging is not necessary Pollination is done the next morning

Peanut plants may be propagated vegetatively Apical stem sections of the peanut plant root in a two week period when treated with a suitable hormone compound [1] Seed yields of cuttings compare favourably with those of original stocks By the use of vegetative propagation several plants may be grown from each hybrid seed obtained Since artificial crossing is difficult and laborious this procedure can save much time for the breeder It also may be used to continue the growth of a plant for a long period of time, or to permit the same plant to be used in successive crosses, or for comparisons of parents with offsprings Vegetative propagation of F_1 plants may also be useful to study the feasibility of using hybrid vigour in peanut breeding

Genetic Studies. The basic haploid chromosome number in the genus *Arachis* is 10,[11] although 5 has also been suggested [18] The cultivated species *A hypogaea* is an allotetraploid with $2n = 40$ chromosomes [12 17] Most of the wild species are diploids with chromosome number of $2n = 20$ Many attempts have been made to produce interspecific crosses within the genus *Arachis* [9 18 22] In general, successful crosses have been made between species at the tetraploid level (*A hypogaea* × *A monticola*) and sterile triploid hybrids with 30 chromosomes have been obtained from crosses between *A hypogaea* ($n = 20$) × *A villosa* ($n = 10$) Crosses between autoploids produced by doubling the chromosome number of diploid species, and tetraploid *A hypogaea* have not yet been successful [23]

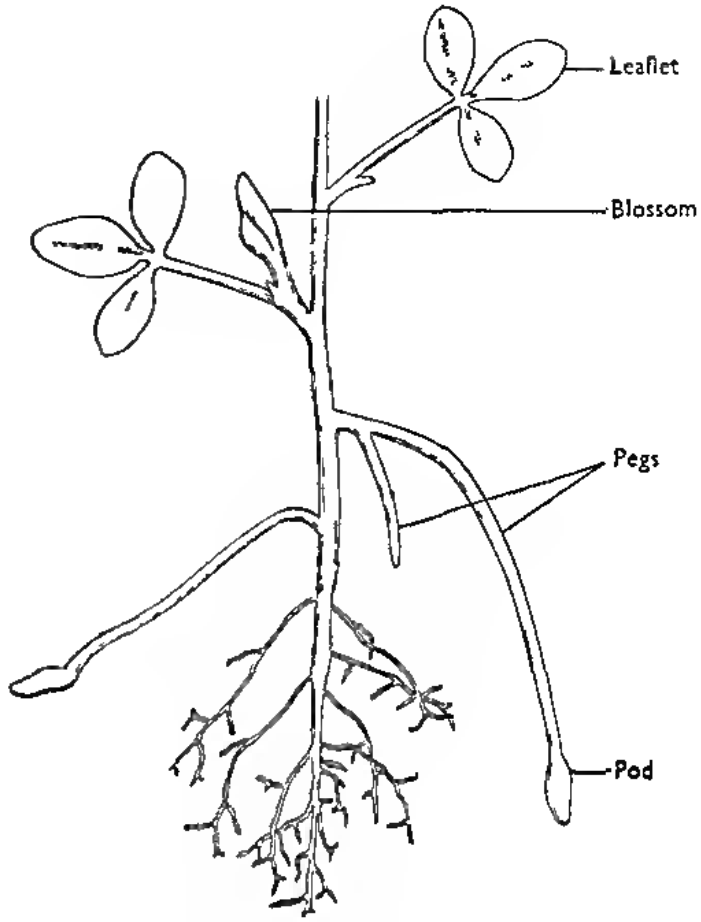


Fig 17 1 Portion of groundnut plant showing (*a*) leaflets (*b*) flower (*c*) pegs and (*d*) developing fruit

Limited genetic studies have been made in groundnut These are related to growth habit, branching duration of the crop pubescence, pod size, seed dormancy disease resistance and other characters [10 18 19] The genetic studies have been limited owing to the difficulty in making artificial crosses With many characters two genes are involved in the inheritance reflecting the tetraploid constitution of the cultivated peanut

Breeding Methods. Introduction, selection and hybridization, as practiced for self pollinated crops, are the principal methods of breeding groundnut Radiation has been used also to induce variations in the groundnut plant

Groundnut strains have been introduced into India and other countries of south and southeast

Asia from Brazil, Africa and the USA Exotic types are being maintained at the Indian Agricultural Research Institute and at other breeding stations in India [3] A selection from an exotic strain from Brazil led to the development of the variety R S B 87 in Rajasthan [2] Pure line selection from local strains led to the improved strain R S 1 in the same state In recent years hybridization between selected local types has been the principal method of breeding groundnuts [20 21]

The groundnut variety NC 4x was released in North Carolina following irradiation of a selection from the variety N C 2 [9] The new strain, NC 4x, outyields the mother strain, N C 2 and is less subject to growth cracks which permit ground water to enter and discolour the kernels The kernel quality of NC 4x is therefore superior to that of the mother strain The development of the NC 4x variety was the outgrowth of a huge groundnut radiation experiment conducted in North Carolina in the U S A In 1949, one bushel of groundnut seed was subjected to x-ray treatment In the R_2 generation, 11,000 visible mutants were observed in 84,213 plants examined [9] Many normal appearing plants, selected at random, were also carried into later generations for study In this experiment an unbelievable range of plant variability was observed [8] These included not only macromutations for phenotypically distinguishable variations in morphological characteristics,[9] vigour and disease resistance,[4] but also micromutants in genotype backgrounds of the deleterious macromutants [5] It appears that the micromutants can be useful to the breeder in selecting for improvement in quantitative characteristics [11]

Breeding Objectives Yield, maturity, plant type, seed dormancy, disease and insect resistance, and quality are the main objectives in breeding groundnut

A YIELD Improvements in yield have been made through pure line selection and hybridization High yield can also be maintained by breeding disease and pest resistant varieties and varieties that respond well to better management practices such as high fertilization and improved water management Shelling percentage must be considered when making yield comparisons of different varieties

B EARLY MATURITY Short duration of the groundnut is favoured by the cultivators to fit into double-cropping patterns Shortage of irrigation water in many areas also necessitates the growing of early varieties

C PLANT TYPE The groundnut may be broadly divided into two plant types, erect and spreading The erect types are grown in irrigated tracts while the spreading types are grown in rainfed or unirrigated areas Heavy branching leads to higher pod formation The pods should not be formed deep in the soil as it makes harvesting difficult and expensive Prostrate habit is dominant over erect, the character being governed by two factors [16] Branching habit is dominant over nonbranching with monogenic inheritance [16] Production of flowers within a short period of time and high seed setting are desirable

D DORMANCY OF SEED Varieties of groundnut vary in dormancy, some germinating immediately after maturity This may result in loss if harvesting is delayed in rainy periods Dormancy is present in some varieties like the spreading variety, T M V 4, of Madras Dormancy in the seed is stated to be partially dominant over nondormancy [10]

E DISEASE AND INSECT RESISTANCE Leaf spot or tikka disease (*Cercospora personata* and *C arachidicola*) and wilt or root rot (*Rhizoctonia destrens*) are the important diseases of groundnut in India Leaf spot, caused by *C personata*, is the most common disease Resistance to each of the leaf spots is independently inherited and a single factor inheritance for resistance to tikka has been reported in wild species like *Arachis villosa* [6 14 21] Hybrids from interspecific crosses have been obtained with resistance to the disease [18] Varieties resistant to leaf spot and wilt include 5203 of Gwalior, G 0120, G 1032 and G 0607 of Mysore, and Exotic 4 of Indore Tai tan and Virginia Jumbo are partially resistant to wilt in the Philippines Schwartz 21 is resistant to the slime disease (*Bacterium solanacearum*) in the East Indies The wild species, *A rasteiro* and *A nambi quarae*, are also reported to be resistant

There is little information about breeding for resistance to insect pests in groundnut

F QUALITY Important components of quality in groundnut include oil content, seed size, seed colour, and shelling percentage Oil content is a major consideration in breeding varieties for oil Varieties used for eating or snacks should have less oil, higher protein and sugar, and larger seed size than those grown for oil There is indication of a negative correlation between seed size and oil con-

tent High shelling percentage is desirable in the groundnut

RAPE AND MUSTARD

The origin of the different rapes and mustards has variously been reported as Asia, Europe and perhaps Africa With the multiplicity of forms that are grown it is quite probable that there were several separate areas of origin Rape and mustard are extensively cultivated in Asia, Japan and western Europe China is the largest producer of rape and mustard and, together with India and Pakistan, they grow over 90 percent of the world production In India, the second largest producer, rape and mustard are grown chiefly in the north Uttar Pradesh grows more than all other states in India combined but important acreages are grown also in Punjab, Rajasthan, Assam, Bihar and West Bengal

Oil extracted from rape and mustard is used almost entirely for edible purposes and is the principal cooking oil in the areas of major production in India The oil content of the seed varies from 30 to 45 percent depending upon the species, the variety, and the climatic conditions under which it is grown The oil cake remaining after extraction of the oil is used as feed for cattle and for manure

Classification. There is much confusion about the names and kinds of rape and mustard that are grown in India, Pakistan, and other countries in south and southeast Asia The same local or vernacular name may be used for different forms and different local names are used for the same form in different areas The nomenclature proposed for the forms of rape and mustard most commonly grown in India and for a related species, *Eruca*, in order to avoid some of this confusion, is given in Table 17 2 [20 21 22] This nomenclature will be followed here (Fig 17 2) Rocket, *Eruca sativa*, is a minor oilseed crop cultivated in some areas and Banarsi rai, (*B nigra*), is a garden crop used for preparation of table mustard Other species cultivated elsewhere as oilseed crops include *Brassica napus* and *Sinapis alba* In western Europe *Brassica campestris* is grown as an oilseed crop but the varieties differ from those grown in southeastern Asia The discussion on breeding here will be confined to rai, sarson and toria Of these sarson and toria (*B campestris*) are the most important

Table 17.2. Nomenclature for Forms of Rape and Mustard Grown in India

General crop name	*Local name*	*Species name*
mustard (Indian mustard)	rai	*Brassica juncea*
mustard (black mustard)	Banarsi rai	*Brassica nigra*
rape (turnip rape)	yellow sarson	*Brassica campestris* var yellow sarson
rape (turnip rape)	brown sarson	*Brassica campestris* var brown sarson
rape (Indian rape)	toria	*Brassica campestris* var toria
rocket (rocket cress)	taramira	*Eruca sativa*

After S ika and Rajan[20] and Singh[21 22]

Only an extremely small percentage of the acreage of these crops is planted to an improved variety

Botany. Rape and mustard belong to the *Cruciferae* family of plants The genus *Brassica* of the *Cruciferae* family contains over 150 species but there is much disagreement about the exact grouping and naming of the various species The *Brassica* species include many common cultivated vegetables, like cabbage, cauliflower, broccoli, turnip, and rutabaga, as well as the cultivated oilseed species

Chromosome numbers of $2n = 16$ 18, 20, 22, 34, 36 and 38 have been reported for different species of *Brassica*[3 4 25] The basic chromosome numbers appear to be 10, 8, and 9 and these genomes have been designated A, B, and C, respectively[9] The chromosome homology and polyploid relationships of a large number of diploid and tetraploid species have been worked out The chromosome numbers and the genome formula for several diploid and tetraploid species of *Brassica* and some related species are shown in Table 17 3 The polyploid origins of the tetraploid amphidiploids, *B juncea*, *B napus*, and *B carinata* were described in Chapter 3 and illustrated in Fig 3 15 This origin has been verified experimentally by crossing the respective diploid species and doubling the chromosome numbers of the F_1 plant produced with colchicine

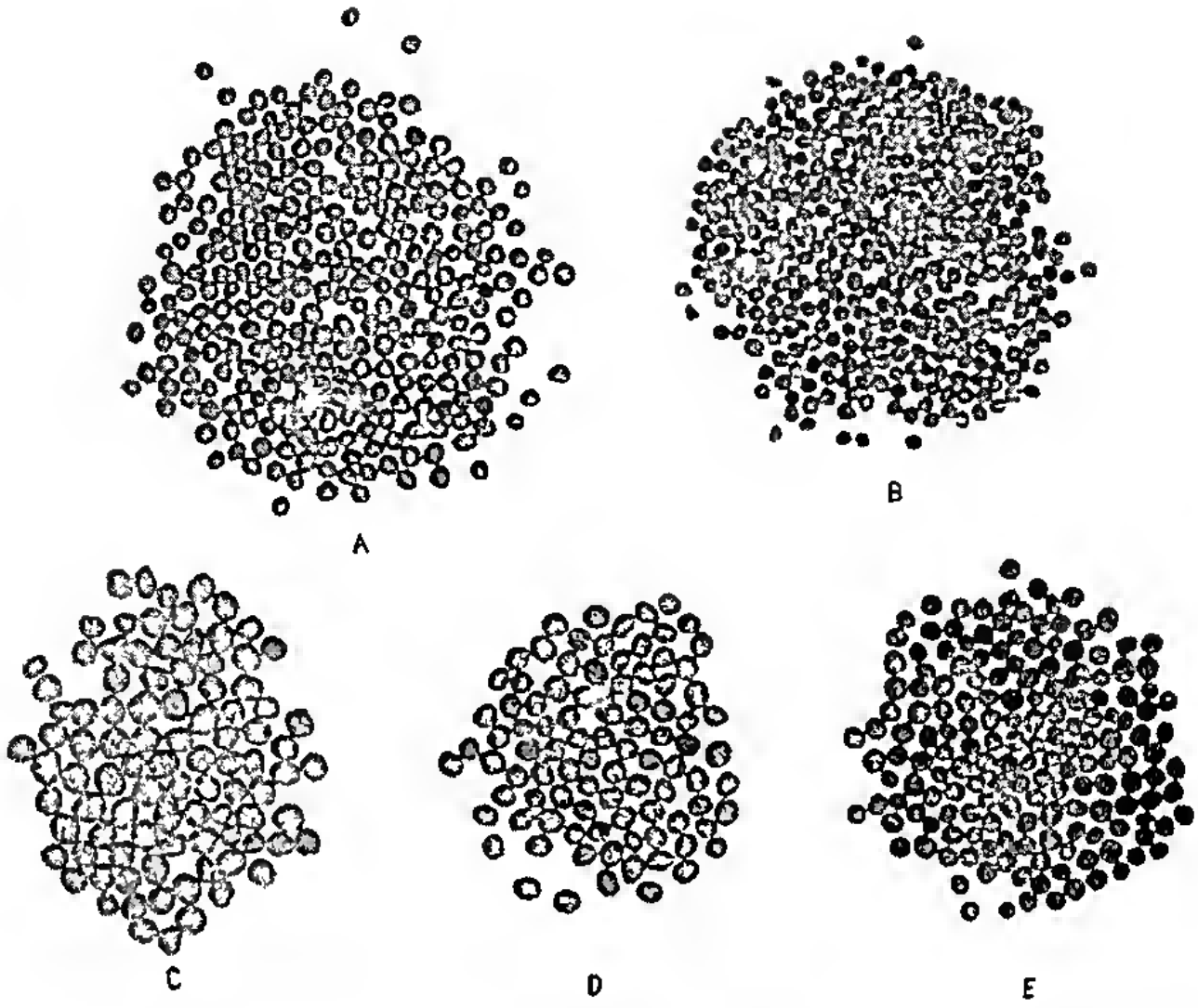


Fig 17 2 Seeds of *Brassica* species and varieties grown in India and Pakistan A Rai (*Brassica juncea*), B Banarsi rai (*Brassica nigra*), C Yellow sarson (*Brassica campestris* var yellow sarson), D Brown sarson (*Brassica campestris* var brown sarson), E Toria (*Brassica campestris* var toria)

thereby producing an amphidiploid The experimentally produced amphidiploid and the naturally occurring tetraploid when crossed produce fertile progenies[9 10 11 24] thereby confirming the polyploid origin of the species

Flowering. Flowers in the *Cruciferae* family are characteristically four petaled, the petals bifurcated with varying degrees of incision and deep yellow to pale yellow or cream in colour There are six stamens four with long and two with short filaments The anthers are lower than the stigmas at bud stage, but prior to flower opening the filaments elongate and carry the anthers upward so that they are as high as or above the stigma [21] The flowers begin to open before 8 A M and continue to open until about noon The flowers remain open for 3 to 4 days after which the petals, sepals and stamens are shed (Fig 17 3)

Varying amounts of self and cross pollination and self and cross incompatibility occur in the different species and strains Mustard or rai (*B juncea*) is self fertile and largely self pollinated Due to insects a certain amount of cross pollination may take place, estimates vary from 4 to 14 percent [6 21] In *B campestris*, yellow sarson and the toria form of brown sarson are self fertile and largely self pollinated although 5 to 12 percent of natural cross pollination may occur in yellow sarson[21] as the result of insects carrying pollen The lotni type of brown sarson and toria are cross pollinated as a result of self sterility It has been shown that in toria the pollen tube requires 24 to 48 hours to

Table 17.3 Chromosome Number and Genome Relationship in *Brassica* and Some Related Species[a]

Species	Chromosome number (2n)	Genome formula	Common name
Diploid species			
Brassica campestris	20	AA	rape turnip rape
Brassica rapa	20	AA	turnip
Brassica chinensis	20	AA	Chinese mustard
Brassica pekinensis	20	AA	Chinese cabbage
Brassica japonica	20	AA	curled mustard
Brassica nigra	16	BB	black mustard
Brassica oleracea	18	CC	kale cabbage
Brassica alboglabra	18	CC	Chinese kale
Brassica hirta	24	DD	white mustard
Eruca sativa	22	EE	rocket salad
Raphanus sativus	18	RR	radish
Tetraploid species			
Brassica juncea	36	AABB	raı Indian mustard
Brassica napus	38	AACC	rape
Brassica napobrassica	38	AACC	swede rutabaga
Brassica carinata	34	BBCC	Abyssinian cabbage

[a] Adapted from Darlington and Wylie [3] Davey [6] Morinaga [9] and Yarnell [25]

reach the ovule in self fertilizations whereas only 5 hours is required with cross fertilization This indicates that the sterility may be due to self incompatibility of pollen and stigma (Fig 3 17) [12] The breeder working with the *Brassica* species will need to study the particular species and varieties with which he is working and learn their fertility relationships and breeding behaviour prior to using them in a breeding project

Fig 17 3 Plants of *B as ica* n bloom at the Indian Agricultural Research Institute New Delh

Emasculation, Crossing and Selfing Techniques Flowers are emasculated in the evening and pollinated the next morning Flower buds that will open the next day are selected and the remainder of the buds and flowers on the flowering branch are removed The petals as well as the stamens of the selected buds are removed with a pair of tweezers and the emasculated flowers are bagged Ripe anthers are collected the next morning and pollinations are made by dusting pollen from the ripened anthers over the stigma After pollination the flowers are again bagged Selfed seed is set freely only in the self fertile species Flowers to be selfed should be bagged before they open to avoid natural cross pollination The bag should be of such size as to allow lengthening of the inflorescence In rape the pollen grains are reported to remain viable for seven days while the stigma is receptive from three days prior to opening of flowers to three days after opening [21] Cross pollination of a group of varieties of the self sterile type of brown sarson or of toria can be obtained by growing them under cages in which are included honey bees or by isolating the varieties at a safe distance from other plantings of the same crop in the field [8]

Genetic Studies and Polyploids There is considerable variability in the plant flower seed pod and seed characteristics of the cultivated and wild species of rape and mustard The inheritance of many of these characteristics has been studied[18 21] but apparently few studies have been made of the inheritance of agronomic characters or disease resistance with utility to the plant breeder

Autotetraploids have been developed by use of colchicine to treat dry seeds or seedling plants in

several of the oilseed species grown in India [12 17] Autotetraploids of toria produced larger seeds than the corresponding diploids but were greatly reduced in seed setting [13] The fertility within the tetraploids has been improved by intercrossing plants selected for improved fertility, employing what is termed a "mass pedigree" system of breeding, but which essentially uses the recurrent selection principle [11] The low seed set in the tetraploids resulted from failure to obtain fertilization of the embryo sac [16] Polyploidy may be used to produce amphidiploids by doubling the chromosome number in F_1 plants between interspecific crosses The synthesis of amphidiploids corresponding to natural tetraploid species, by crossing diploid species and then doubling the chromosomes in the resulting F_1 plants, was described in Chapter 3

Interspecific crosses in *Brassica* have been made by many workers with varying degrees of success depending upon the genome homology Intra species crosses indicate that genome homology between toria and brown sarson is closer than between toria and yellow sarson [21]

Breeding Methods. Breeding methods for any crop must take into consideration the self and cross fertility relationships and the breeding systems within the species In rape and mustard there are self fertile forms of yellow sarson and toria brown sarson, (*B campestris*), and rai (*B juncea*), and self-sterile forms of toria and lotni type brown sarson (*B campestris*) Even in the self fertile forms cross pollination is extensive ranging from 5 to 15 per cent In this regard these crops are like cotton in which considerable cross pollination normally occurs, and it would therefore appear that breeding procedures similar to those used in cotton could be successfully employed These would include such basic procedures as mass selection, progeny selection, and hybridization to combine genes for useful characteristics In the self sterile and cross pollinated forms, procedures commonly employed in the breeding of cross pollinated forage crops would appear to be most appropriate These include mass selection, recurrent selection, utilization of synthetics, and hybridization

A INTRODUCTION AND GERM PLASM COLLECTIONS Initially it is desirable to assemble as large a collection of types and varieties as practical to be used as a source nursery These may be obtained from collections made in farmers' fields, by utilization of stocks already available in breeding nurseries, or by introduction of strains from other countries Maintenance of these collections in *Brassicas* poses two problems, (*a*) the production of seed by selfing and self-pollination in view of the self sterility problems in many species, and (*b*) the prevention of cross pollination between the various strains growing in the breeding nursery The breeder will need to screen the source nursery to find high yielding types, disease resistance, desirable plant types and seed quality

B SELECTION Various selection procedures may be used in the breeding of rape and mustard Three methods are listed below They have been discussed in detail in Chapter 4 and in chapters on breeding specific crops

(*1*) *Pure line* selection may be used in the self fertile species to isolate superior lines Possible reduction in vigour must be considered, and bagging to prevent outcrossing carried out to keep the lines pure

(*2*) *Mass selection* may be used to increase uniformity or to obtain improvement for a particular character in cross pollinated species The procedure was used in Punjab to develop strains with earlier maturity, larger seed size, and higher protein content

(*3*) *Progeny selection* based on progeny performance would be superior to mass selection which is based on phenotypic appearance only This procedure is outlined in detail in the chapter on cotton A similar selection procedure has been described as "mass pedigree" system by some oilseed breeders [19]

(*4*) *Recurrent selection* procedures should prove useful in improving quantitatively inherited characteristics in the cross pollinated forms

C SYNTHETIC VARIETIES Development of synthetic varieties, utilizing the polycross technique to identify lines with superior combining ability, may be used with cross pollinating types and varieties The polycross technique will be described in detail in Chapter 18 on Breeding Forage Crops Selfing for one generation before the polycross test is conducted has been found to be useful in increasing homozygosity for certain characters [19] It will be necessary to save part of the seed from each selfed plant put into the polycross for possible later use in making up the synthetic Plants to be combined in the synthetic are chosen on the basis of

their combining ability as learned from testing the polycross progenies [7] Development of synthetic varieties appears to be a practical and effective method of breeding rape and mustard

D HYBRIDIZATION Hybridization may be used to combine the superior characteristics of two or more strains The recurrent selection procedure may be utilized to concentrate genes for quantitative characters such as oil content by group hybridization of selected strains

Use of hybrid vigour and production of hybrid seeds by use of self incompatibility genes have been suggested [23] but a workable procedure has not so far been developed With suitable cytoplasmic male sterility and restorer genes, utilization of hybrid vigour might be feasible

E USE OF POLYPLOIDY Studies on polyploidy in toria have been continued in the Indian Agricultural Research Institute, New Delhi, for a long time [13 14 16 17] The autotetraploid toria produced heavier seeds with more oil content but the percentage of seed set was low By suitable selection procedures types with higher seed set are being isolated [14] Polyploidy is being used in Western Europe in some of the *Brassica* species used as root crops to develop higher yielding types (Fig 3 16)

F MUTATION BREEDING Irradiation may be used as a tool for creating variability or to induce mutations for specific characters desired in a variety

Objectives in Breeding Rape and Mustard

The main objectives in breeding rape and mustard are yield, plant type, shattering resistance, disease resistance, insect resistance, and quality

A YIELD The average yield of rape and mustard in India is rather low Although poor water management and inadequate use of fertilizer are major causes of low yield, there is plenty of scope to increase yield by breeding superior varieties Larger seed size and higher oil content of seeds are important considerations in breeding for increased yield as well as ability to set more seeds The contribution of secondary branches to yield is stated to be more important than that of tertiary and subsequent branches Hence, selection for number of secondary branches and for number of pods per secondary branch may lead to the selection of higher yielding types

Yield is also directly related to disease and insect resistance Aphids in particular result in yield losses which might be reduced by breeding aphid resistant forms

B PLANT TYPE Plants with compact branching are preferred to lax types The latter type tends to fall down and makes harvesting difficult Further, tertiary and subsequent branching does not contribute much toward yield

C SHATTERING RESISTANCE The pods have a tendency to dehisce in most varieties which leads to loss in the field before and during harvest It is desirable to introduce genes for shattering resistance to the adapted varieties so that the pods will hold the seed for a sufficient time after maturity to permit harvesting with a minimum of loss

D DISEASE RESISTANCE Several diseases are found on rape and mustard in the fields *Alternaria* blight, caused by *Alternaria brassicae*, is the most destructive [20] No breeding work for resistance to disease has been done in India and sources of resistance are still unknown

E INSECT RESISTANCE Like disease resistance insect resistance in rape and mustard has received little or no attention Two important pests of the crop are aphids (*Lipaphis erysimi*) and mustard sawfly (*Athalia proxima*) [20 22] Autotetraploid toria is reported to have increased resistance to aphids [15]

F QUALITY Important characteristics of quality are oil content of the seed, and taste and colour of the oil There is much variability within existing varieties in oil content which indicates that this characteristic could be improved with breeding Seed colour is related to colour of oil Brown seeded toria gives dark coloured oil and yellow seeded varieties give light coloured oil Brown seed colour is dominant over yellow Pungency in the oil is preferred in northeastern India while a sweeter taste is preferred elsewhere [20]

Rape or mustard seed oil varies in the proportion of fatty acids present Erucic acid is a major constituent of rapeseed oil, the content of which varies with the variety A high content of erucic acid is desirable for certain industrial uses By contrast rapeseed oil with low erucic acid content is similar to groundnut or soybean in composition In crosses between a high erucic acid variety and a strain with zero erucic acid the F_1 was intermediate [5] Gas liquid chromatographic analysis techniques have been developed which utilize only a single cotyledon from a seed [5] It is therefore possible to remove one cotyledon from a seed, test the erucic

acid content, and plant the remainder of the seed containing the embryo With this technique early generation segregating populations may be analyzed and only genotypes selected for desired oil content carried forward Previous techniques required producing several pounds of seed of a strain before tests for fatty acids could be made

BREEDING SESAME

Sesame also called *til* and *gingelli*, is one of the oldest of the cultivated oilseed crops The origin of sesame is variously reported from southern Africa to central Asia, but the diversity of wild species growing in Africa would tend to favour its origin in that location [5] Sesame has been cultivated for centuries in India, Pakistan, Burma, Indo China, China, Japan and Africa In more recent times sesame has been introduced into Mexico, Central America, South America and the U S A India grows about 40 percent of the world production, with China second in production Nearly 60 percent of the world s acreage is in India Burma, and Pakistan In India the crop is grown chiefly in the central states both as a kharif and rabi crop

Sesame seeds provide an important source of cooking oil as well as being eaten directly as food The oil is nearly colourless, odourless, and remains liquid at low temperatures and for this reason may be used as a salad oil in cool climates Sesame oil does not become rancid easily, and may be used to absorb the fragrant essence of sweet scented flowers as a base for perfumes

Classification. Since sesame has been grown in widely different geographic areas for such a long time it is not surprising that a multitude of forms have evolved Various varietal classifications have been worked out[7 9 11] separating varieties on the basis of maturity (early vs late), season of cultivation (kharif vs rabi), seed colour, number of flowers per leaf axil, and number of carpels (two vs four) None of these classifications appear to be very useful to the plant breeder except for minor identification purposes

Botany and Genetic Studies Sesame belongs to the genus *Sesamum* of the *Pedaliaceae* family More than 36 species have been described in the genus *Sesamum* In addition to *Sesamum indicum*, the cultivated sesame, two wild species, *S prostratum* and *S laciniatum*, are found in India Species of *Sesamum* may be divided into three groups on the basis of chromosome numbers as follows [5]

Group	*Chromosome number*	*Examples of species*
Group I	$2n = 26$	*S indicum* *S alatum*
Group II	$2n = 32$	*S prostratum* *S laciniatum*
Group III	$2n = 64$	*S radiatum* *S occidentale*

The flower of sesamum has a two lipped, tubular corolla with five lobes which are united at the base [3] The corolla varies from white to purple in colour and is covered with short hairs Four stamens are grouped in two pairs with one pair of stamens shorter than the other [9] Flowering occurs in early morning with the anthers beginning to dehisce around 3 A M shortly before the flowers open The stigma becomes receptive with the dehiscence of the anthers and remains so until 7 or 8 A M The stigma is usually covered with pollen by day break when insect visitation begins, so self pollination is the rule [5] However, pollen carried by insects may result in some cross pollination, usually around 5 percent [6 11] The corolla withers and falls off towards the afternoon

Genetic Studies. Limited genetic studies have been made in sesame [5 11] These studies have been concerned mostly with simple morphological characters A few studies have been made of inheritance of important agronomic or disease resistance characters useful to the plant breeder [3 4 12] Many interspecific and a few intergeneric crosses have been attempted Interspecific crosses of *S indicum* ($n = 13$) with *S prostratum* and *S laciniatum* ($n = 16$) have been successful if the amphidiploid was produced by doubling the chromosome number of the F_1 hybrid Autotetraploids of *S indicum* have been produced which exhibit gigas characters but they are late in maturity and poor in fertility [8]

Selfing and Crossing Technique. Artificial crossing procedures resemble the soda straw technique used with cotton [2 6] The corolla tube and

attached unopened anthers may be removed by hand leaving the pistil intact A soda straw is slipped over the pistil in late afternoon and folded tightly at the free end Ripe anthers are rubbed over the stigma the following morning It is desirable to bag the flowers when selfing to ensure freedom from natural crossing by insects

Breeding Methods. Breeding methods commonly used for self pollinated crops may be used for breeding sesame These include introduction, selection, and hybridization The initial step in breeding sesame would be to collect as many types as possible from different sources and survey the breeding materials available Selection within these lines may isolate pure line types with special characteristics related to high production or quality As soon as good characters are identified in individual lines, hybridization may be used to combine the best qualities of two or more lines into a single strain Interspecific crosses and backcrossing may be utilized for incorporating desirable genes into the cultivated species or superior varieties Until breeding stocks with superior characters have been exhausted, recombination breeding would appear to be more feasible than utilization of mutation or polyploidy techniques

Objectives in Breeding. Breeding sesame has received attention in India, U S A Venezuela, and other countries Major objectives in breeding are yield, early maturity, shattering resistance, disease and insect resistance, and quality

A YIELD Isolation of pure lines from local types has led to development of varieties in India like Punjab Til No 1 A few selections, like TMV 2 and TMV 3 of Madras, have been released as a result of hybridization With proper selection of parents, there is possibility for increasing yield through hybridization

At the India Agricultural Research Institute, New Delhi, emphasis has been on the development of nonbranching varieties with capsules borne on the main stem or with clusters of pods in the leaf axils so as to permit growing of a larger plant population per unit area (Fig 17 4) Branching habit is dominant over unbranched habit and a single gene difference between the characters has been suggested [5] Similarly, single pods are dominant over multi pods with monogenic inheritance [4 13] Sources for these characters are available among the cultivated varieties

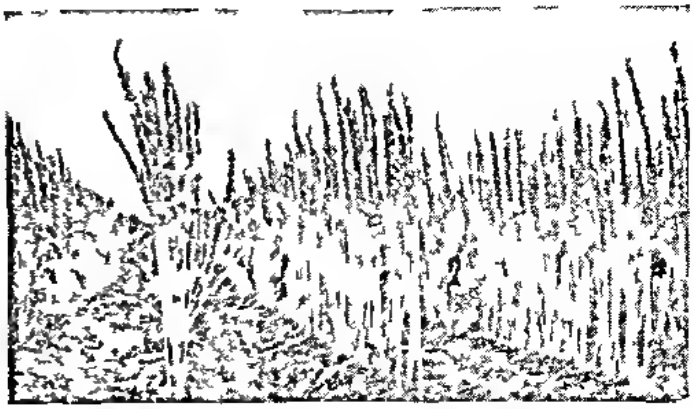


Fig 17 4 Plants of a nonbranching variety of sesame with leaves removed to show the prolific production of seed pods

B EARLY MATURITY Varieties of sesame vary in their maturity period from 80 to 150 days Early maturing varieties are preferred if yields are not adversely affected by the early maturity Varieties, like TMV 2 and TMV 3 of Madras, No 10 of Uttar Pradesh, and N P 3 and N P 7 from the Indian Agricultural Research Institute, are early in maturity Earliness and lateness is controlled by a single pair of genes

C SHATTERING RESISTANCE Shattering of seeds is a major problem in sesame The pods dehisce at maturity and shatter causing loss of seeds during harvest and in handling Nonshattering types found in Venezuela have been introduced into the U S A for breeding nonshattering varieties[2] (Fig 17 5) Indehiscence of pod is found to be recessive to dehiscence Besides one major gene, some modifying genes are reported

D DISEASE AND INSECT RESISTANCE A host of diseases, phyllody, leaf curl, leaf spot (*Cercospora sesami*) anthracnose (*Colletotrichum sp*), *Fusarium* wilt (*Fusarium vasinfectum*), root and stem rot (*Macrophomina phaseoli*), and bacterial leaf spot (*Pseudomonas sesami*) have been recorded on sesame Little is known regarding sources of disease resistance in India Resistance to bacterial leaf spot has been reported in the U S A but the resistance broke down with the appearance of a second race of the *P sesami* organism [12] The variety Early Russian is resistant to race 2 Attempts have been made in India to transfer resistance to phyllody, a virus disease, from *S prostratum* to the cultivated sesame [10]

Among insect pests of sesame, resistance is known for the til leaf roller, *Antigastra catalaunalis* The wild

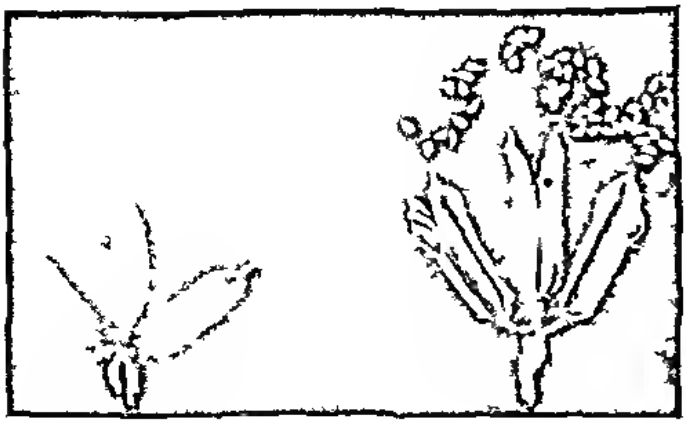


Fig 17 5 Pods of nonshattering (indehiscent) and shattering (dehiscent) sesame

species *S prostratum* is reported to be resistant to this pest

E QUALITY Oil content and colour and size of seed are important in measuring quality The oil content of existing varieties ranges between 45 to 60 percent The colour of the seed appears to be related to oil content and white seeded varieties have higher oil content than the brown or black seeded varieties Bold seeded varieties are also preferred to small seeded ones Oil content is a polygenic character although a relatively few genes are reported to control its inheritance [8] In the same study heritability values for oil and protein content were reported to be 50 and 60 percent, respectively If a relatively few genes are involved and heritability is high rapid progress in improvement of oil content should be possible

BREEDING LINSEED (FLAX)

Linseed belongs to the *Linaceae* family It supplies either oil or fibre but different varieties are grown for the two purposes Linseed originated in south western Asia[5] and the Mediterranean area of Europe and has been cultivated for over 5 000 years In the process of evolution the early maturing types grown in the more tropical climates of Asia became the oil bearing types while the linseed of the cooler European climates developed into the fibre bearing types

India is third among all countries in acreage of linseed behind Argentina and the U S S R The linseed plant is grown primarily for oil but is harvested for fibre in some areas in India The fibre produced in a tropical climate is poorer in quality than that produced in a cool climate India has become one of the major linseed oil exporting countries Linseed oil is a drying oil and is used in paints and varnishes The linseed crop is unsuited to growing during periods of high rainfall and is generally planted at the end of the rainy season using water stored in the soil for its growth and development

Botany and Genetic Studies The commercial varieties of common linseed belong to the species *Linum usitatissimum* The genus *Linum* consists of about 100 species which are widely distributed in the subtropical and temperate climates of the world Little is known about the genetic relationships of these species and interspecific crosses have for the most part been unsuccessful The commercial species *L usitatissimum*, has a chromosome number of $n = 15$ In other species of the genus *Linum* haploid chromosome numbers of 8, 9, 10 12 14 15 and 16 have been identified, with $n = 9$ the most common number and $n = 15$ the next most common number [7 31]

The linseed flower has five petals which may be white blue violet purple, or pink The linseed boll is five celled, with two seeds normally produced in each cell or ten seeds per boll Three boll types dehiscent semidehiscent, and indehiscent are distinguished [6 10] The indehiscent characteristic permits the linseed to stand in the field with less loss from shattering or damage from water absorption before harvesting [10]

The linseed flower begins to open and the anthers shed pollen shortly after sunrise The flower is fully open by 7 A M and the petals fall before noon [8] The linseed flower has five anthers and a pistil with five slender styles (Fig 17 6) Linseed is normally self pollinated although 0 3 to 2 percent natural crossing has been observed [9 18 26] the amount varying with the variety the season and the number and kinds of insects present Plants in the breeding nursery may be covered with cotton bags to prevent natural crossing (Fig 17 7)

Artificial cross pollinations are easily made The linseed flower shows a cone of colour on the afternoon preceding opening and emasculations are made late that afternoon or early evening The cone of petals is removed by pulling gently with the thumb and index finger Then one or two sepals are rolled back and held down while the five anthers are removed with the point of a pencil or fine pointed tweezers Care must be exercised to

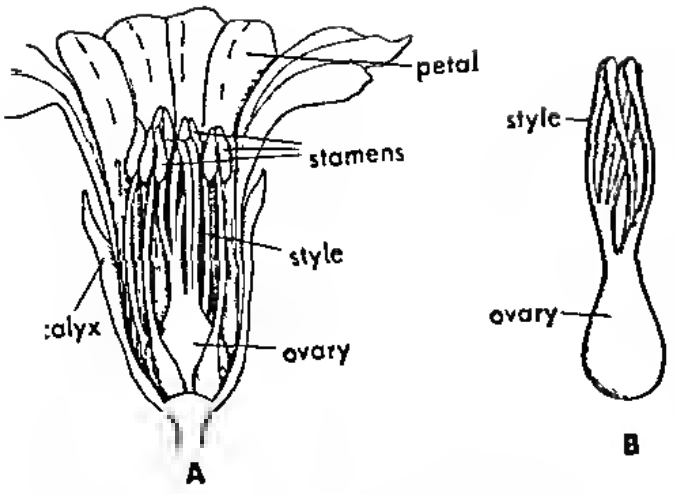


Fig 17 6 Flower of linseed A Longitudinal section through a flower of linseed showing the calyx petals five stamens and pistil B Pistil with five styles.

Fig 17 7 Linseed breeding nursery at the Indian Agricultural Research Institute New Delhi Plants at right are bagged to ensure self pollination At left Dr B R Murty and Dr M S Swaminathan inspect the linseed plots In the background a crop of *B assica* is in blossom

prevent injury to the stigma or it will dry out rapidly It is unnecessary to cover emasculated flowers since insects are not attracted to the flower after the petals have been removed The emasculated flowers may be marked by tying tags or small pieces of coloured string about the petiole Different colours may be used on different days or to mark different crosses

Pollinations are made the morning after emasculation usually before 8 A M Delay in pollinating may result in a poor seed set because the pollen dries out and deteriorates rapidly Petals are removed from the flowers selected to supply the pollen and their anthers are brushed lightly over the stigmas of the emasculated flowers One male flower will pollinate two or three emasculated flowers

About five flowers open on a plant each day during the full bloom period It is thus possible to work several flowers on a plant in one day With careful emasculation correct timing of pollination and good weather a high percentage of flowers will set seed with an average of five to seven seeds per boll The linseed plant usually blooms over a long period of time so further pollinations may be made if the first ones fail

Extensive genetic studies of linseed have been made [8 34 36] Many have dealt with simple morphological characteristics seed colour and other characters In the United States genetic studies have been directed largely toward the inheritance of disease resistance and quality Extensive studies have been made in India on disease resistance

Tetraploid forms have been produced by treatment of seedling plants with colchicine [32] The tetraploid plants produced larger seeds but were later in maturity reduced in fertility and lower in yield and oil content than the corresponding diploids

Early studies on linseed varieties in India were made by Howard and Khan [20] Both brown and yellow seeded varieties of linseed are now grown (Fig 17 8) In the U S A a classification of linseed varieties was made by Dillman [10]

Methods of Breeding The methods of breeding linseed are introduction selection and hybridization as used for other self pollinated crops A large collection of varieties including introductions from Afghanistan Greece Germany France Holland Sweden U S S R U S A Canada Argentina and Australia are maintained at the Indian Agricultural Research Institute New Delhi Interspecific crosses have been utilized in breeding for disease resistance [3] The backcross technique may be used to add specific genes as discussed in Chapter 4 on breeding methods Autotetraploids have not been successful A natural mutation for yellow seed colour led to the development of the variety N P 124 which was released as a high yielding type

Consideration is being given in the U S A and elsewhere to the possibilities of hybrid linseed production [2] Hybrids 25 to 40 percent above

Fig 17 8 Seed of linseed types grown in India A Bold brown seeded variety B Small brown seeded variety C Yellow-seeded variety

the best parent have been reported Cytoplasmic sterility and gene restorer systems are available in linseed These might be utilized in hybrid linseed production by procedures similar to their utilization in maize sorghum bajra and wheat but several difficulties regarding pollen dispersal must first be overcome Linseed pollen is heavy and sticky and not wind blown and its distribution will be dependent upon insects mainly bees The pollen is shed only during a few hours each morning The petals fall off of the flowers before noon and flowers without petals are unattractive to bees Thus pollen distribution must be accomplished within a short period in the early morning Also male sterile flowers tend to be smaller in size and remain closed and are therefore less accessible to insect pollinators However varieties C 1150 C 1193 1 and N P (R R)204 were found to have open flowers even though they were male sterile

Breeding Objectives The improvement of linseed for the past half century has been centred around the breeding of disease resistant varieties [8 25 37] In few other crops has the objective of disease resistance occupied so great a portion of the breeder s attention for so long a period Other major objectives in breeding linseed are yield maturity and quality of oil Each will be discussed briefly

A YIELD Many varieties have been developed in India with improved yield In these varieties disease resistance made a major contribution to their good performance [25] Seventy five percent of the linseed in India is grown in the central and peninsular agroclimatic regions and varieties for each of these zones are needed It has been found that profusely branching varieties with bold seeds yield higher than less branched small seeded types Oil content as well as seed yield is a factor in total oil production

B MATURITY Maturity is an important consideration in adaptation of varieties to specific areas Early maturity is needed to fit varieties into double cropping and special cultivation patterns

C DISEASE RESISTANCE The pioneering work on disease resistance of linseed was done by Bolley in the U S A [1] 'From a plot of diseased linseed growing on flax sick soil' Bolley in 1901 isolated the fungus that causes the wilt disease in linseed (*Fusarium lini*) From surviving wilt resistant plants he developed the first wilt resistant variety Later he found some of the wilt resistant strains to be resistant also to linseed rust [38] Rust and wilt resistance breeding in India started in the 1940 s Some collections of linseed varieties received from Australia were tested for resistance to rust and strains with the accession numbers Al 2 Al 3 and A17 1 1 were found to be resistant [21] These strains had originated from lines developed earlier by Bolley in the U S A for wilt and rust resistance From crosses of these strains with Indian varieties linseed rust and wilt resistant strains adapted to India like N P R R 9 have been developed [21 25]

The linseed rust organism *Melampsora lini* has many specialized physiologic forms and 570 races were isolated in the U S A from field collections during the period 1931 to 1951 [13] Since then a new system of classifying linseed rust races has been devised based on the reaction of specific differential varieties each of which apparently carries a single rust conditioning gene [15 16 17] Genes conditioning

rust resistance in linseed have been found at five loci Until other loci are found the breeder cannot incorporate more than five genes for resistance into a single variety

An intensive study has been made of the inheritance of resistance to linseed rust in linseed varieties and also of the inheritance of virulence in the linseed rust organism [12 14 15 16] From inbreeding studies with the linseed rust organism it was learned that linseed rust races in common with races of other rusts are frequently heterozygous Virulence (the ability of the disease organism to produce infection in a variety) is with one known exception inherited as a recessive character in linseed rust In heterozygous races a gene for virulence may be masked by a dominant gene for avirulence (lacking ability to incite infection) In the linseed plant genes for resistance are dominant It has been proposed that for each gene for resistance or susceptibility in the linseed plant there is a corresponding gene for avirulence or virulence in the linseed rust organism [14 15 16 17] This is called a gene for gene relationship With this concept a linseed rust race that attacks many linseed varieties would possess a large number of genes for virulence Also a linseed variety would be attacked only by a race of linseed rust with the specific gene or genes for virulence to that variety New linseed rust differentials have been developed in line with this concept so that each possesses a single gene for rust resistance

A survey of 574 samples of linseed rust from 10 states of India during 1946 to 1959 revealed the presence of five physiologic races [33] None of these races had been identified previously A sixth race was identified in 1959 60 [28] Sources of rust resistance to these races have been identified [29 30] Resistance of N P R R 82 and N P R R 202 to linseed rust is conditioned by a single dominant gene and resistance of N P R R 200 and N P R R 204 is conditioned by two dominant duplicate genes [27 21] Inheritance of resistance to wilt in Bolley Golden variety of linseed has been reported to be conditioned by two complementary genes [23 27] Genes for powdery mildew resistance are now being added to wilt and rust resistant varieties

D QUALITY Oil content and iodine number are two important components of seed quality They may be influenced by environmental conditions in which the linseed is grown as well as the hereditary characteristics of the plant [11] Large seeded varieties have higher oil content but oil from small seeded varieties has a higher iodine number [3] Yellow seeded varieties are superior to brown seeded varieties in oil content and iodine number [4] and the oil has a clearer colour A yellow seeded mutant N P 12 which arose in the N P 11 variety has been used in the development of yellow seeded varieties in India The yellow seed coat colour is recessive to brown colour

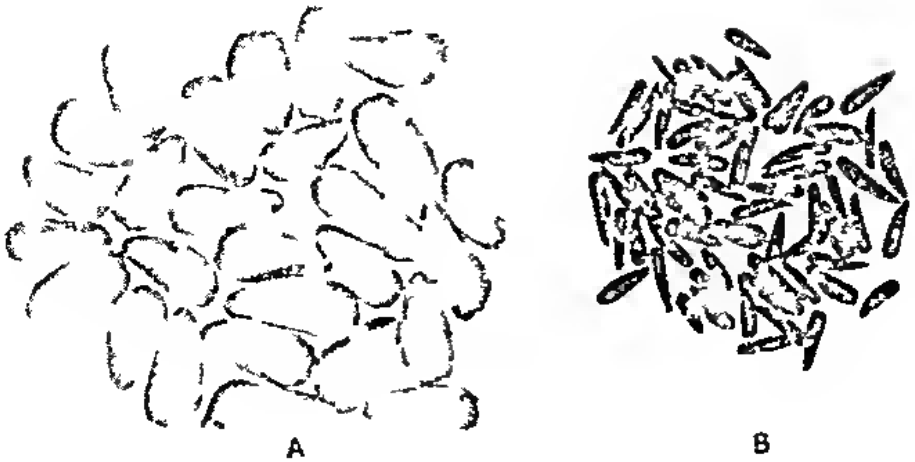
BREEDING SAFFLOWER

Safflower has been grown for many centuries from Egypt in north Africa eastward to India (Fig 17 9) Based on the diversity of plant types safflower is believed to have two centres of origin Ethiopia and Afghanistan [3] India is the largest producer of safflower and grows well over 75 per cent of the total world acreage [9 10] Madhya Pradesh Maharashtra Andhra Pradesh Mysore Bihar West Bengal and Uttar Pradesh are all important safflower producing states

The flower of the safflower has a brilliant yellow to orange or orange red colour Dyes like carthamin and safflower yellow may be extracted from the florets of safflower For centuries the safflower plant was an important source of these dyes but this usage has declined since synthetic dyes may now be produced more cheaply In India safflower oil is used primarily for cooking and lighting Safflower oil is becoming more popular as an edible oil in many countries since it has a high degree of polyunsaturation Safflower oil is utilized also in the manufacture of soap alkyd resins and other types of drying oils The young plants are sometimes used as fodder

Botany and Genetics Cultivated safflower *Carthamus tinctorius* is a much branched herbaceous annual growing 1 to 2 feet in dwarf types to 3 or 4 feet in tall types (Fig 17 10) The inflorescence is typical of the *Compositae* the family to which safflower belongs except that the ray florets are absent Varieties vary widely in morphological characters A total of 63 safflower types in India have been described by Howard *et al* [6] Khan,[8] Sabnis *et al* [14] and Chavan [3]

The diploid chromosome number in cultivated safflower *C tinctorius* is $2n = 24$ About 25 valid species of *Carthamus* are recognized with diploid chromosome numbers of 24, 44 and 64 [2]



A B

Fig 17 9 A Seed o safflower (*Carthamus tinc tor us*) B Seed of nige (*Gu zotia abyssin ca*)

chromosome numbers a e 10 and 12 Two w ld species are found in Ind a *C oxyacantha* (2*n* — 24) and *C lanatus* (2*n* 44) The progenitor of cultivated safflower has not been determined

Interspecific crosses have been made between *C t nctorius* and other species with corresponding chromosome number *C palaestinus* and *C oxy acantha* [1] Inheritance of a large number of characters —cotyledon shape cotyledon colour leaf margin sp nes corolla colour and seed shattering—were monogen cally controlled in the crosses

Studies in India on natural crossing in safflower reported an average of 10 to 15 percent although individual plants varied from 1 to 28 percent [6 7] In the U S A individual plants were found to vary from 0 to 100 percent natural crossing although most plants outcrossed from 5 to 40 percent [4] The amount of natural cross pollination varies with the plant the flower colour and the insects present Wind is ineffective as a pollinating agent natural crossing resulting almost wholly from in sect carried pollen

Artificial crosses are difficult to make [3 6] Anthers are removed in the bud stage 12 to 24 hours before normal dehiscence Emasculated florets are rinsed with water or a 57 percent ethyl alcohol solution followed by a water rinse to remove pollen grains shed during the emasculation process Emasculated florets are pollinated the next morning

Due to the natural cross pollinat on in safflower bagg ng of heads is necessary in the nursery to ensure maintaining purity of strains Butter paper bags may be used for this purpose

Breeding Methods Breeding methods that may be usefully followed in safflower include intro duction pure line selection mass selection progeny selection and hybridization These procedures have been described in previous chapters and will not be repeated here

Breeding Objectives The objectives in breed ing safflower are high seed yield desirable plan

Fig 17 10 Plant of safflower show ng leaves branching hab t of growth and flower heads

type, frost and drought resistance, disease and insect resistance, and quality

A YIELD High yield of seed is the primary objective in order to obtain a higher outturn of oil High seed yield will be determined by the size and number of flowers per plant, percentage of seed set, and seed size or weight Yield is also influenced by the disease and pest resistance, and resistance to frost and other adversities hence these characters also need attention while breeding for high yield An important factor leading to lower yield is sterility in flowers, thus resulting in reduced seed set Sterility is due to lack of normal development of floral parts and can be improved through selection [13]

B PLANT TYPE A desirable plant type would be one with good branching the branches arising from the lower level of the main stem, early and uniform maturity, resistance to shattering, and spineless inflorescence Spineless inflorescence helps in harvesting Uniform flowering is also important for efficiency in harvesting

C FROST AND DROUGHT RESISTANCE Since the crop is grown during the rabi season starting in October, it may be affected by frost in parts of north India Breeding varieties resistant to frost would prevent loss of the crop in such regions Safflower is grown mostly in low rainfall areas and in unirrigated tracts and varieties need ability to grow and produce under drought conditions With increasing facilities for irrigation in the country, however, the importance of this character will gradually decline Early maturity is important in escaping drought or in efficient utilization of irrigation water in irrigated areas

D DISEASE AND INSECT RESISTANCE Rust (*Puccinia carthami*), root rot (*Phytophthora drechsleri*), leaf spot (*Cercospora carthami*), Alternaria leaf spot (*Alternaria carthami*), and wilt (*Sclerotinia sclerotiorum*) are common diseases of safflower [3 5 10 14] Very little work on breeding for disease resistance has been done in India Certain varieties from Turkey and Romania have shown resistance to rust in the U S A [3] A variety resistant to Phytophthora root rot, U S 10, has been released in the U S A [15] A new safflower line U-1421, developed in Utah, is resistant to the two common strains of Phytophthora root rot and to all races of rust in the U S A Several insect pests cause heavy damage to the crop, however, information on insect resistance is not available

E QUALITY High oil content, large seed size and low husk percentage are important qualities that deserve consideration in a breeding programme If used as a fodder, qualities like succulence and high protein content would increase the nutritive value

In recent years there has been an increase in interest in cooking oils with a high level of polyunsaturation The level of unsaturation is measured by the iodine value of the oil, which in commercial safflower varies from 138 to 145 [11] The polyunsaturation in safflower oil is provided by a high content of linoleic acid which in most strains averages around 76 percent Search for strains with a higher percentage of linoleic acid has not been fruitful but recently strains from India tested in the U S A were found which have a lower iodine value than the American varieties with which they were compared Inheritance of low iodine value was controlled by a single recessive gene, *ol* The genotypes *olol*, *Olol*, and *OlOl* produced seeds with iodine values of 75 to 90, 111 to 130, and 131 to 145 respectively Analysis of the fatty acid content of single seeds can be made using gas chromatographic techniques The studies indicate that the genotype of the seed is important in determining the fatty acid content of the seed, rather than the genotype of the plant that produces the seed [11]

BREEDING CASTOR

Castor is an oil yielding crop which may be grown in tropical subtropical, or temperate climates Castor is believed to be indigenous to Africa but the crop is widely grown in southern Asia and in South America It is also grown in China, Thailand U S S R and the U S A India is the second largest producer after Brazil and accounts for nearly 30 percent of the total world production [5] Madras, Andhra Pradesh, Gujarat, Mysore, Madhya Pradesh, Uttar Pradesh, Bihar, and Orissa are the states with the largest acreage Both cultivated and wild forms are found throughout India

There is a wide range of use for castor oil The oil is used in adhesives, plastics, soaps, lubricants, printing ink, waxes, rubber substitutes, drying oil for enamels, paints and varnishes, cosmetics, and pharmaceuticals The plant itself may be used as a source of pulp for cellulose, cardboards, and newsprint The oil cake is poisonous for cattle but

may be used as fertilizer Most of the castor oil produced in India is exported

Botany and Genetic Studies The castor plant, *Ricinus communis* belongs to the family, *Euphorbiaceae* In the tropical and subtropical areas the castor plant grows as a perennial and may attain heights of 20 to 30 feet but in the temperate climates its growth is terminated by frost and it grows as an annual (Fig 17 11) [12] The somatic chromosome number in *R communis* is $2n = 20$ Castor has been reported to be a polyploid with a basic chromosome number of $n = 5$ [6] The castor plant is normally monoecious with about 50 to 70 percent male flowers occurring towards the base of a racemose inflorescence and 30 to 50 percent pistillate flowers in the upper portions (Fig 2 4) Variations in this pattern of flowering include (*a*) racemes with pistillate and staminate flowers interspersed throughout (*b*) racemes with 70 to 90 percent pistillate flowers (*c*) racemes with 100 per cent pistillate flowers, and (*d*) racemes with a few hermaphroditic flowers [5] The 90 to 100 percent pistillate character which is used in the production of hybrid castor is controlled by a major recessive gene The stability of sex expression varies with the environment [8] The flowers are wind and insect pollinated and from 5 to 46 percent natural cross pollination has been reported in normally monoecious strains [4 7]

Artificial pollination and emasculation are not difficult For emasculation the male flowers are removed from the inflorescence and the female ones can be pollinated by dusting with the desired pollen The inflorescence should be bagged to protect it from foreign pollen (Fig 17 12) Likewise bagging is required to ensure selfing For experimentally producing hybrid seed the planting of a natural crossing plot and removal of staminate inflorescences by hand from one variety has been suggested [11] This procedure may be practical on a small scale where parent varieties are of similar maturity Two methods have been proposed for utilization of the pistillate flowering characteristic for the commercial production of F_1 hybrid seed [3] (*a*) Utilize inbred lines which breed true for 90 to 100 percent pistillate flowers as female parents Since a small amount of hybrid or selfed seed would occur, the hybrids thus produced would not be entirely uniform (*b*) Utilize plants with 100 percent pistillate flowers in lines segregating one heterozygous monoecious to one dioecious plant The heterozygous monoecious plants are rogued out of the crossing blocks before flowering begins The female plants remaining are pollinated with a selected male line planted in a ratio of 1 male to each 6 or 8 female rows The latter method has been used commercially [12]

Fig 17 11 Plants of castor variety P C No 1, developed at the Punjab Agricultural University Ludhiana At left is Dr D S Athwal who assisted in the development of the variety

Genetic studies on castor have dealt with many characters such as stem colour, echinate nature of stem capsule characteristics, dwarf internodes, early maturity, seed colour, spiny fruits, character of inflorescence, and others [5 7]

Breeding Methods Breeding procedures used with castor must take into account the various flowering types and the fact that both self and cross pollination normally occur Selfing or inbreeding castor does not appear to be followed by a reduction in vigour, so inbreds (pure lines) may be evaluated and utilized either directly as varieties or as parents in hybrid combinations

As with other crops collection and survey of existing germ plasm sources is an initial step in the breeding of castor Since many varieties of castor have been maintained under open pollination, selection and purification may be an essential first step, which may lead to superior varieties Punjab Castor No 1, recently released in Punjab state, is an increase from a local strain, selected after 120 varieties had been evaluated Hybridization may

Fig 17 12 Flowers of castor bagged to prevent cross pollination

be used to obtain genetic recombination and create new populations from which superior varieties or inbred lines may be obtained and backcrossing may be used to add a superior character to a variety or inbred Recurrent selection should be a useful tool for concentrating genes for specific characteris tics in open pollinated populations Such popula tions could be used as sources of inbreds after several cycles of recurrent selection

Current emphasis on breeding is being directed to the development of F_1 hybrids, using strains with a high percentage of pistillate flowers on the female line, according to procedures already described Hybrid vigour has been noted in seedling vigour, seed yield oil content, and seed weight [9 13] Breed ing hybrid castor requires that inbreds be devel oped with both a high degree of pistillateness and high combining ability

Breeding Objectives. Yield early maturity, plant types adapted to more efficient harvesting, disease and insect resistance, and seed quality are the principal objectives in breeding castor

A YIELD Breeding for high seed yield has been the primary objective in breeding castor in India Rapid, vigorous early growth is indicative of high yield Large, densely crowded, fruiting racemes are generally looked for in high yielding types As emphasis on breeding hybrid castor increases, combining ability of the inbred lines must be evaluated

B MATURITY Early high yielding varieties of castor are desirable to fit it into double cropping systems The crop is grown during three seasons in south India and earliness helps in fitting the crop to specific cultivation patterns Uniformity of seeds is also desirable

C ADAPTATION TO EFFICIENT HARVESTING The difficulty of harvesting castor has been a factor in the low acreage of this crop Shattering resistance, dwarf internode plant types, strong stems and uni-form maturity of capsules would all contribute to ease and efficiency in harvesting Dehiscent cap-sules result in a loss of seed before harvest Develop-ment of nonshattering varieties would reduce this loss The variety TMV 2 from Madras is reported to have nondehiscent capsules Dwarf internode varieties are used in the U S A for mechanized harvesting of castor

D DISEASE AND INSECT RESISTANCE Very little research has been carried out on disease and insect resistance of castor in India Resistance to these maladies will result in increased yield The variety TMV 3 of Madras is reported to be resistant to bacterial wilt and the stem borer (*Dichrocrocis punctiferalis*) Several indigenous forms and an Italian variety have been reported to be resistant to mites [1] Varieties in the U S A are reported to be resistant to bacterial leaf spot and to Alternaria leaf spot

E QUALITY Oil content seed size, and thin capsules or shells are important in breeding for improved quality High oil content has been a major consideration in most breeding of castor Oil content varies from 35 to 60 percent in the cultivated varieties The improved variety of Punjab, Punjab Castor No 1, has an oil content of 54 percent while the perennial variety of Madras, Co 1, is reported to have an oil content of 59 per-cent Small seeded varieties tend to be higher in oil than the large seeded varieties Oil content is influenced by climate and maturity as well as variety A thin shell in the capsule is also desirable in an improved variety

BREEDING NIGER

Niger, a native of Africa, is an annual herbaceous plant with seeds used for extracting oil or for edible purposes Although it is cultivated also in Africa, West Indies and Germany, the most extensive cultivation of niger is in India The states with the largest acreages are Madhya Pradesh, Andhra Pradesh, Orissa Maharashtra and Mysore [1] The oil of niger is used for lighting and cooking purposes A portion of the seed is exported to England, France, and other countries where the oil is used in making soap and in the preparation of cooking fats

Botany and Genetic Studies Niger, *Guizotia abyssinica* belongs to the *Compositae* The inflorescence is typical of the *Compositae* family Each head produces about 20 seeds which are small and black when mature (Fig 17 9) Twenty to forty or more flowers are borne in a single plant The somatic chromosome number is $2n = 30$ [3] Niger is essentially a cross pollinated crop [1 2] The flowers start opening about 8 A M , the ray florets opening earlier than the disc florets The flowers in the outer whorl open first and the process continues inward The period of flowering of a head may continue for 7 or 8 days Hand pollination when selfing gives better seed set than simply bagging the head The ray florets, which are pistillate flowers, may be selected for artificial cross-pollinations and emasculation avoided by removing the other florets No genetic study of important economic character has been reported

Breeding Methods. Very little breeding work has been done in niger Mass selection, progeny selection, development of synthetic varieties, hybridization and recurrent selection may be used for improvement of the crop

Breeding Objectives. High yield, uniform and heavy flowering, nonshattering and high oil content are some of the important objectives in breeding niger Information about resistance to diseases and pests is also needed

BREEDING SOYBEAN

For many centuries soybeans have been an important food crop in China, Japan, and adjacent areas Although introduced into the U S A in the latter part of the 19th century their production remained largely as a minor fodder crop until as late as 1940 Since 1940 there has been a shift in emphasis toward harvesting the soybean crop for seed in the U S A (Fig 17 13) The increase in acreage there has since been phenomenal While less than 5 million acres were harvested in the U S A for beans in 1940, the harvested acreage today is nearly 30 million acres and the soybean now rivals maize in the Corn Belt and cotton in the Cotton Belt in importance and value

Soybeans in the U S A are used primarily for oil and protein Nearly 90 percent of the soybean oil consumed in the U S A is used for cooking oil and for margarine and 95 percent of the protein is used as feed for livestock Large quantities of soybean oil are exported The great increase in acreage has resulted from (*a*) the high potential acre yield for both oil and protein of the soybean crop, (*b*) the breeding of improved oilseed varieties, (*c*) the utilization of the protein in livestock feed particularly for poultry and swine, and (*d*) the ease of production and high yield of soybeans as compared to other oilseed crops

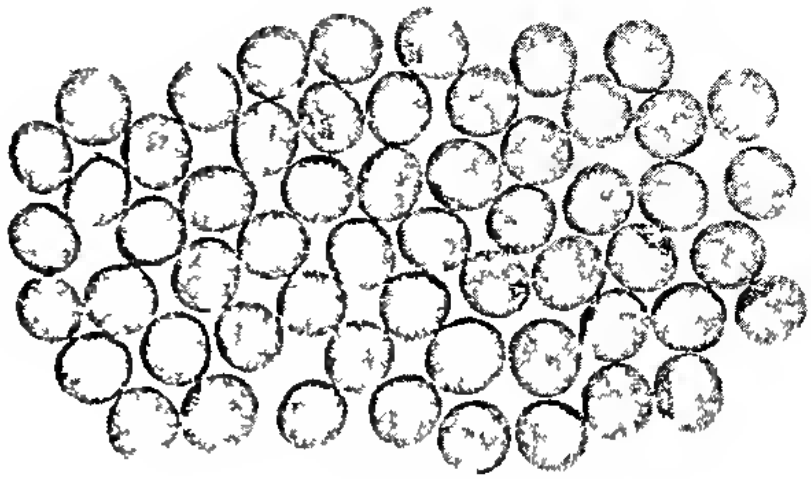
In India only a few thousand acres of soybeans are grown The small acreage has apparently resulted from (*a*) failure to breed varieties adapted to India's climate, (*b*) lack of technological research in developing the industrial utilization of soybeans as an oilseed crop, and (*c*) preference for pulses to the soybean as a proteinaceous food However, in view of the potential for high oil production in the soybean crop and the fact that thousands of tonnes of soybean oil are now being imported into India, it seems that the breeding of soybean varieties adapted to India's climate might well be taken up on a large scale In addition to the oil, the soybean meal, owing to its high protein, may be effectively utilized in baby foods, or for livestock feed, particularly for poultry and broiler production, thereby improving the nutritional level of the Indian diet

Botany of the Soybean. The soybean, *Glycine max*, belongs in the family *Leguminosae* There are 10 species in the genus *Glycine* according to a recent revision [1] *Glycine max* has a chromosome number of $2n = 40$ Other species of *Glycine* have chromosome numbers of $2n = 20$ and $2n = 40$, with a basic number of 10 The soybean originated in China, with *G ussuriensis* as a probable progenitor [2]

The cultivated soybean is self-pollinated with only a slight amount of natural cross pollination

Breeding Methods. Introduction, selection, and

17 13A



17 13B

Fig 17 13 Soybean (*Glycine max*) A Plants of soybean B Seeds of soybean

hybridization have been the principal breeding methods[3] In the U S A the backcross has been used to concentrate genes for quantitative characters such as high yield lodging resistance and high oil content

Breeding Objectives The major breeding objectives have been high seed yield maturity to fit the area of production nonshattering pods stronger stems disease and nematode resistance and improved quality[3] Most improved soybean varieties are adapted to a narrow range of latitude owing to their photoperiod sensitivity Varieties introduced into India from the U S A are sometimes unadapted and perform poorly as a result of the differences in photoperiod Varieties from southern U S A usually perform better in India than varieties from northern U S A It will be necessary to select varieties with suitable photoperiod response for Indian conditions Improved strains from Taiwan and the Philippines where breeding projects are in progress may be better adapted than strains from the U S A

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18

Breeding Forage Crops

Little attention has been given in the countries of south and southeast Asia either to the cultivation or the breeding of forage crops Pressure of large populations, food shortages and small farm units has necessitated concentration on food crops such as cereals, pulses, oilseeds and sugarcane, or high value cash crops such as jute, cotton, and tobacco Fodder production has been only incidental to the production of food crops After the seed was threshed from the paddy or millets or pulse crops, the straw or stover was used as livestock feed Seldom is a crop grown primarily for use as hay or fodder A similar situation exists with respect to pasture Many cattle and other livestock are grazed on unimproved forest areas, roadsides or vacant areas On the small acreages cultivated by many villagers, tillable land cannot be spared from its use in producing human food

As advanced agricultural practices are adopted —irrigation, high fertilizer applications, and improved varieties—food production can be substantially increased over the present low levels of production This change would permit land to be released from cultivation for food and be used for forage or fodder production and would permit greater emphasis on animal production Improved cultural practices, improved varieties of forages, and improved livestock will mean greater returns to the cultivator and, of greatest importance, an improvement in the nutritional level of the peoples' diets as more animal proteins are eaten For this reason some consideration to the breeding of forage crops needs to be given here

Progress in forage breeding made the most rapid progress in the early part of this century in Great Britain and the Scandinavian countries of Europe Many basic methods and techniques were developed by their work This was followed by a marked increase of attention to forage breeding in the U S A , Canada, and New Zealand Most of the examples cited in this chapter will be drawn from these sources Many of them necessarily will be with species neither grown nor adapted to the countries of south and southeast Asia They will serve, however, to illustrate the progress that can be made and the methods by which such improvements can be achieved.

WHY FORAGE CROP BREEDING IS DIFFICULT

Breeding forage crops is more difficult than breeding cultivated crops The difficulties arise from the methods of pollination in the forage species, the irregularities in fertilization and seed setting, and problems concerning the evaluation and maintenance of new strains Examples are

1 Most important forage species are cross pollinated The heterozygosity in cross pollinated species makes it difficult to propagate and maintain the identity of lines

2 Many forage species are largely self sterile, and therefore are limited in the extent to which they may be inbred

3 Many forage species have small floral parts This makes artificial hybridization difficult

4 Certain grasses reproduce largely by apomixis (seed setting without fertilization)

5 Many forages are poor seed producers, or produce seed of low viability

6 Many forages produce weak seedlings, and it is then difficult to establish stands

7 It is often difficult to find clean land on which to increase new strains without danger of mixing

8 The initial evaluation of selected plants or lines is based on the performance of spaced plants, or rows, which may not accurately represent the

performance of the strain in a thickly seeded stand as grown by the cultivator

9 Forage species are often sown in mixtures which complicate the evaluation of single species

10 Strains may perform differently with different systems of grazing management

11 Most forages are long lived perennials and require many years to evaluate persistence and productiveness of new strains

Due to the paucity of agronomic information on forage species adapted to south and southeast Asia and the pollination patterns and breeding behaviour of those that may be adapted, the lack of experience by breeders in working with these crops, and the lack of germ plasm collections from which to draw breeding materials, progress at first can be expected to be slow

FORAGE SPECIES IN INDIA

A comprehensive review of the systematics of the grasses of Burma, Ceylon, India and Pakistan has been compiled by Bor and will be useful to the forage worker of south and southeast Asia in learning about his natural resources [7] A survey of the grasslands of India was carried out by the Indian Council of Agricultural Research It has been suggested that India be divided into five ecological zones for the study of forage species [28] The zones and some forage species promising in each are as follows

(1) Arid tract of Rajasthan and adjoining areas
grasses *Cenchrus ciliaris, C setigerus, Panicum antidotale, P turgidum, Elyonurus hirsutus*
legumes *Indigofera, Crotalaria*

(2) Humid and subhumid tracts of north and northeast India
grasses *Bothriochloa pertusa B intermedia, Paspalum dilatatum, Desmostachya bipinnata, Chrysopogon aciculatus, Ischaemum arristatum*

(3) Semiarid tracts of south and central India
grasses *Sehima nervosum, Chrysopogon montanus, Dichanthium annulatum, D caricosum, Heteropogon contortus*

(4) Subtropical and temperate regions in foot hills of Himalayas
grasses *Arundinella* spp , *Themeda anathera, Chrysopogon montanus*
legumes *Atylosia* spp

(5) Alpine and subalpine regions
grasses species of *Bromus, Poa, Festuca, Calamagrostis, Dactylis, Agrostis*
legumes species of *Trifolium, Medicago, Melilotus, Lotus.*

Cultivated cereal crops which may be used as fodder include, sorghum, bajra, maize, oats, and millets Also used as forage are several legume crops such as groundnut, *Vigna, Dolichos* spp , *Phaseolus* spp and others Our discussions in this chapter will pertain generally to the species used primarily as forages, rather than to the cultivated cereals or legumes cultivated primarily for their seeds for which breeding procedures have already been discussed

POLLINATION, FERTILIZATION, AND SEED SETTING

Pollination and fertilization vary with different species of forage crops Although there are exceptions, most of the annual species of grasses and legumes are self-pollinated, and most of the perennial species are cross pollinated Information on the normal mode of pollination, chromosome number, and growth habit of some important cultivated species of grasses and legumes, many from the western world, are listed in Table 18 1

Flowering and Seed Setting in Forage Grasses. Wind is the principal pollinating agent of cross pollinated species of forage grasses (Fig 18 1) Blooming begins near the apex of the inflorescence and progresses more or less regularly toward the base The flowers of many grasses bloom most abundantly during the early morning but some species bloom, or have an alternative period of blooming, in the afternoon Blooming is favoured by sunshine and temperatures of 21 degrees Centigrade or above and is hindered by cool or cloudy weather [60] Injury to the pollen or abnormal drying of the stigma may result from high temperatures during the summer months

The annual self pollinated species of forage grasses set seed more or less freely after self fertilization The perennial cross pollinated species vary considerably in this respect This may be demonstrated by bagging heads to exclude foreign pollen and comparing the number of seeds set in the bagged and in open pollinated heads on the same plant Care must be taken that the temperature within

Table 18.1. Mode of Pollination or Seed Setting, Chromosome Number, and Growth Habit of Some Cultivated Species of Forage Grasses and Legumes[a]

Species	*Crop*	*Chromosome[b] number (2n)*	*Growth habit*
	Normally self pollinated forage grasses		
Agropyron trachycaulum	slender wheatgrass	28	short lived perennial
Sorghum vulgare var sudanense[c]	sudangrass	20	annual
	Normally self pollinated forage legumes		
Dolichos biflorus	kulthi, horsegram	24	annual
Lespedeza striata	common lespedeza	22	annual
Vicia sativa	common vetch	12, 14	annual
Vigna unguiculata	cowpea	22, 24	annual
	Normally cross pollinated forage grasses		
Agropyrum cristatum	crested wheatgrass	14 28	perennial
Agrostis alba	redtop	28, 42	perennial
Bromus inermis	smooth bromegrass	28, 54 58	perennial
Cenchrus ciliaris	anjangrass	36	perennial
Chloris gayana[d]	rhodesgrass	20, 40	perennial
Cynodon dactylon	bermudagrass	36, 40	perennial
Dactylis glomerata	cocksfootgrass, orchardgrass	28, 42	perennial
Eremochloa ophiuroides	centipedegrass	18	perennial
Festuca pratensis	meadow fescue	14	perennial
Lolium perenne	ryegrass	14	perennial
Panicum antidotale	blue panicgrass	18	perennial
Panicum maximum[d]	guineagrass	18, 22, 36, 44, 48	perennial
Paspalum dilatatum[d]	dallisgrass	40	perennial
Paspalum notatum[d]	bahiagrass	20, 40	perennial
Pennisetum purpureum[d]	napiergrass, elephantgrass	27, 56	perennial
Pennisetum typhoides	bajra, pearl millet	14	annual
Phleum pratense	timothy	56, 70	perennial
	Normally cross-pollinated forage legumes		
Lotus corniculatus	birdsfoot trefoil	24	perennial
Medicago hispida	burr clover	14	—
Medicago parviflora	senji, Indian clover	—	—
Medicago sativa	lucerne, alfalfa	16, 32, 64	perennial
Melilotus alba[e]	sweetclover	16, 24	biennial
Trifolium alexandrinum	berseem, Egyptian clover	16	perennial
Trifolium pratense	redclover	14	biennial
Trifolium repens	white clover	32	perennial
Trigonella foenum graecum	fenugreek	16	—

[a] Adapted from Carnahan and Hill,[8] Hanson and Carnahan,[37] Johnson,[39] Myers,[41] Patil *et al* [45] Vinall and Hein [60]

[b] Various chromosome numbers are reported in some species by different workers because of variations between plants and errors in determining chromosome numbers

[c] Partially cross pollinated [d] Partially apomictic [e] Partially self fertile

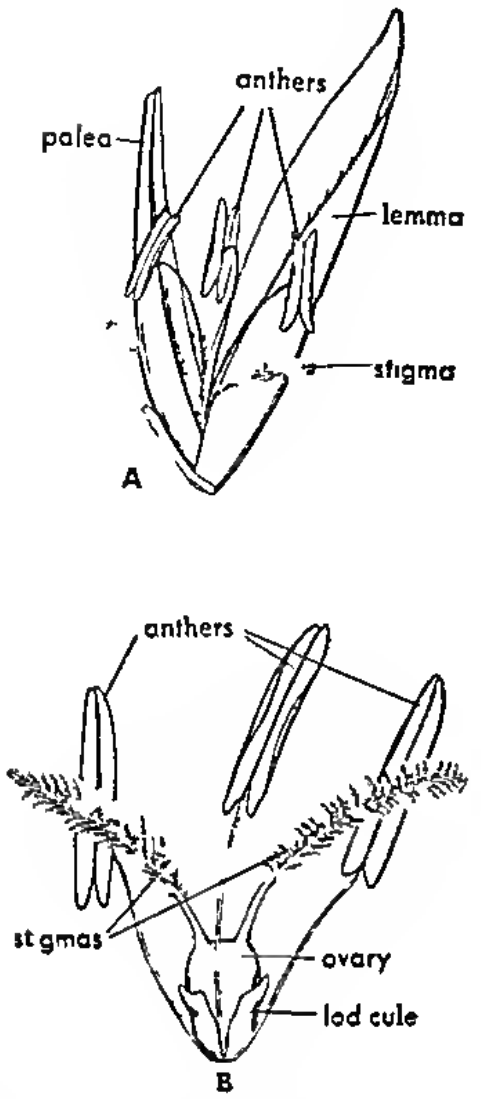


Fig 18 1 Grass flower A Typical floret at time of blooming The lemma and palea have been forced open by the swelling of the lodicules and the stigma and the stamens have been exposed permitting cross-pollination B Essential organs in grass flower

the bag does not become so high as to reduce seed setting

Self incompatibility is a factor in seed setting following self pollination in many species of grasses In some grasses there are two incompatibility loci S and Z[34] Identity of alleles in pollen and pistil at both loci results in incompatibility Details of self incompatibility systems are known in four diploid species of grasses *Secale cereale*, *Festuca pratensis*, *Hordeum bulbosum* and *Phalaris coerulescens* Self incompatibility imposes restrictions on inbreeding in species containing the incompatibility alleles

Restrictions on both inbreeding and cross breeding are imposed by apomixis which is more or less common in the *Gramineae*[35] Many genera from the tropical and subtropical regions, particularly *Bothriochloa Paspalum Pennisetum*, *Urochloa*, and *Dichanthium* contain species known to be apomictic From the temperate region, the genera *Poa*, *Eragrostis*, and *Calamagrostis* contain apomictic species

Procedures have been developed for the artificial self pollination and hybridization of grasses The small size of forage grass spikelets makes emasculation and artificial crossing more tedious than with the cereal grains although the procedure is similar[47] To control pollination, inflorescences are enclosed in bags or sleeves made of cloth or butter paper (Fig 18 2) Bagging procedures used with different selfing and crossing techniques[5] are as follows

1 Inflorescences of plants to be *self pollinated* are bagged without emasculation

2 Inflorescences of plants to be *artificially cross pollinated* are bagged separately Pollen is then collected from the male parent and transferred to the emasculated female parent

3 *Controlled natural cross pollinations* may be made by enclosing unemasculated inflorescences of two plants in the same bag A high degree of self sterility is depended upon to prevent selfing

Seed set of bagged heads in 1 and 3 above can generally be improved by shaking the bag during the period of pollen shedding to disseminate the pollen Contaminations with foreign pollen may be reduced by making emasculations and hand pollinations inside a draught proof glasshouse Sometimes emasculations are made by chilling or by hot water treatments which kill the pollen[31] Different species require different temperatures for successful emasculation by the hot water method but temperatures around 45 to 48 degrees Centigrade for periods varying from one to five minutes are commonly employed

Flowering and Seed Setting in Forage Legumes In self pollinated legumes such as the pulses the pollen is shed directly upon the stigma when the anthers open In the cross pollinated legumes different types of pollinating mechanisms are present in different legumes The forage crop breeder must become familiar with the flower structure and the pollinating mechanism in the species with which he is working Three types of pollinating mechanisms in legume flowers will be described here In each, selfing is largely prevented by a high degree

Fig 18 2 Bagging selected plants of bromegrass *Bromus inermis* in a breeding nursery in the U S A

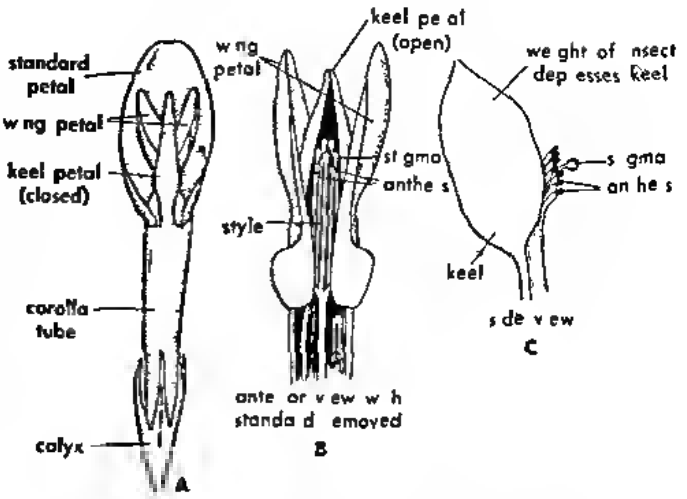


Fig 18 3 Flower structure and pollinating mechanism in red clover *Trifolium pratense*

of self sterility This will be discussed in more detail later

In red clover *Trifolium pratense* nine stamens are fused to form a tube which encloses the stigma and the tenth stamen remains free (Fig 18 3) The stigma protrudes slightly above the anthers at the time of flowering The keel petals form a receptacle enclosing the staminal tube with a small opening at the tip At the base of the tube is the nectar When an insect alights on the keel and inserts his proboscis down into the flower to obtain nectar the weight of the insect s body presses down the keel exposing the anthers and the stigma Pollen carried by the insect is dusted over the stigma and fresh pollen is rubbed off onto the insect from the anthers which will be carried to the next flower it visits When the insect leaves the flower the keel returns to its former position and conceals the anthers From four to eight insect visits are required to exhaust the pollen supply of a flower Bees are the principal pollinators of red clover

In birdsfoot trefoil *Lotus corniculatus* pollen is dispersed by means of a piston apparatus The keel petals conceal the anthers and the stigma and form a conical cavity above the anthers with a small hole in the apex of the cone (Fig 18 4) The anthers dehisce inside the keel and fill the cone with a mass of sticky pollen When the insect alights on the flower and depresses the keel from the weight of its body, the stamens are forced up into the cone with a piston like movement The pressure compresses the pollen and forces a ribbon of it out through the opening in the apex of the cone The sticky pollen covers the underside of the insect Further depression of the keel will cause the stigma to protrude where it will be covered with foreign pollen carried by the insect When the pressure on the keel is removed the organs return to their normal position Pollen may be pumped from a particular flower as many as eight times if the keel is not depressed too low

In lucerne *Medicago sativa* pollen is dispersed by an explosive action commonly known as *tripping* The keel petals which are held down under tension conceal the staminal column (Fig 18 5) When the keel is pressed down by the weight of the insect the stamens and stigma are snapped upward and free of the keel with a force similar to that produced by the release of a spring under tension (Fig 18 6) The insect is struck by the staminal column often unseating him and his underside is covered with a mass of sticky pollen which is carried to the next flower it visits (Fig 18 7) There some of the pollen is rubbed on the stigma and more pollen is added to his load Lucerne flowers are usually tripped by bees although automatic tripping by wind rain or heat may occur occasionally A flower may be tripped by hand by using a small object such as a toothpick or the point of a pencil to apply a light pressure on the keel Bees are the most important insect pollinators of lucerne Cross pollinated flowers of lucerne set seed more freely than selfed flowers There is considerable variation in the ability of individual lucerne plants to set seed after selfing Some selfed lines have a high degree of self fertility and others a high degree of self sterility or incompatibility [58] Higher seed set

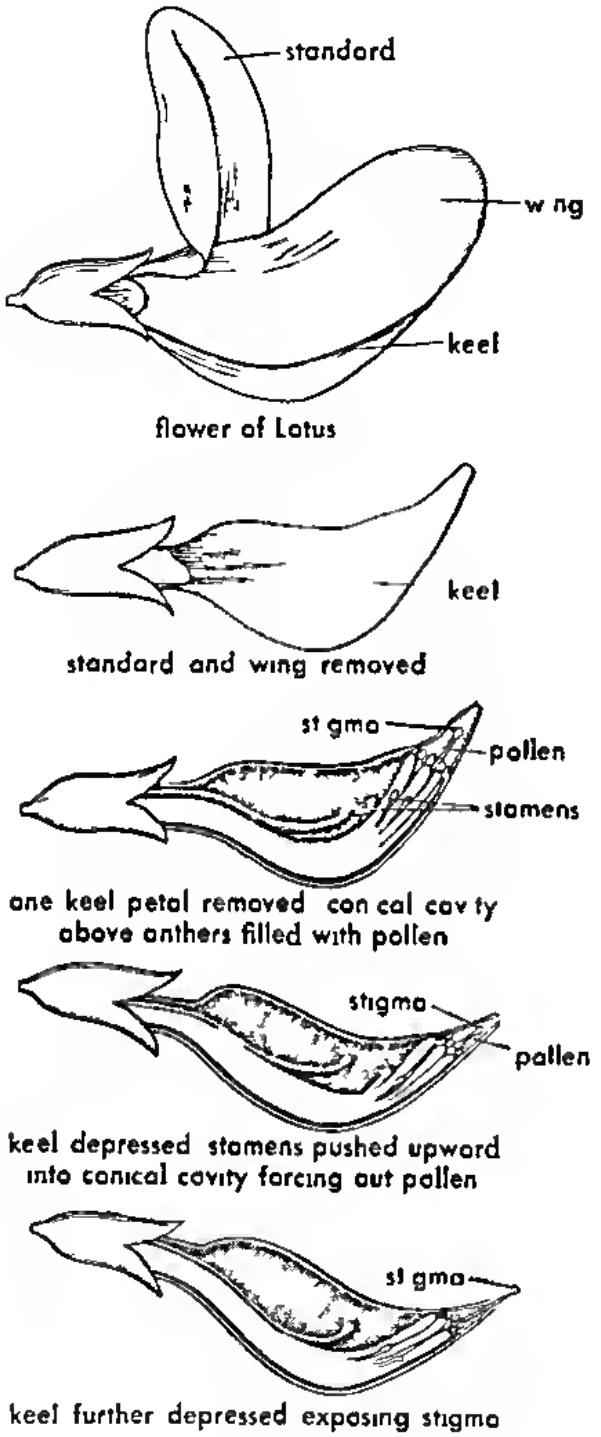


Fig 18 4 Flower structure and pollinating mechanism in *Lotus corniculatus*

is obtained in lucerne with cross pollination than with self pollination because (*a*) pollen tube growth is more rapid with foreign pollen (*b*) self pollen is partially incompatible (will not fertilize an ovule of the same plant), and (*c*) embryos abort and fail to develop more frequently after self fertilization than after cross fertilization [11]

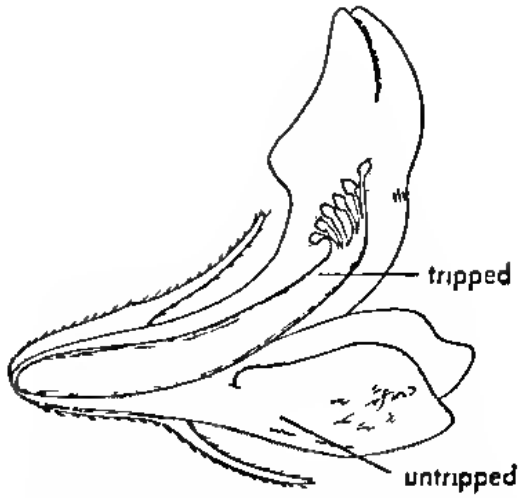
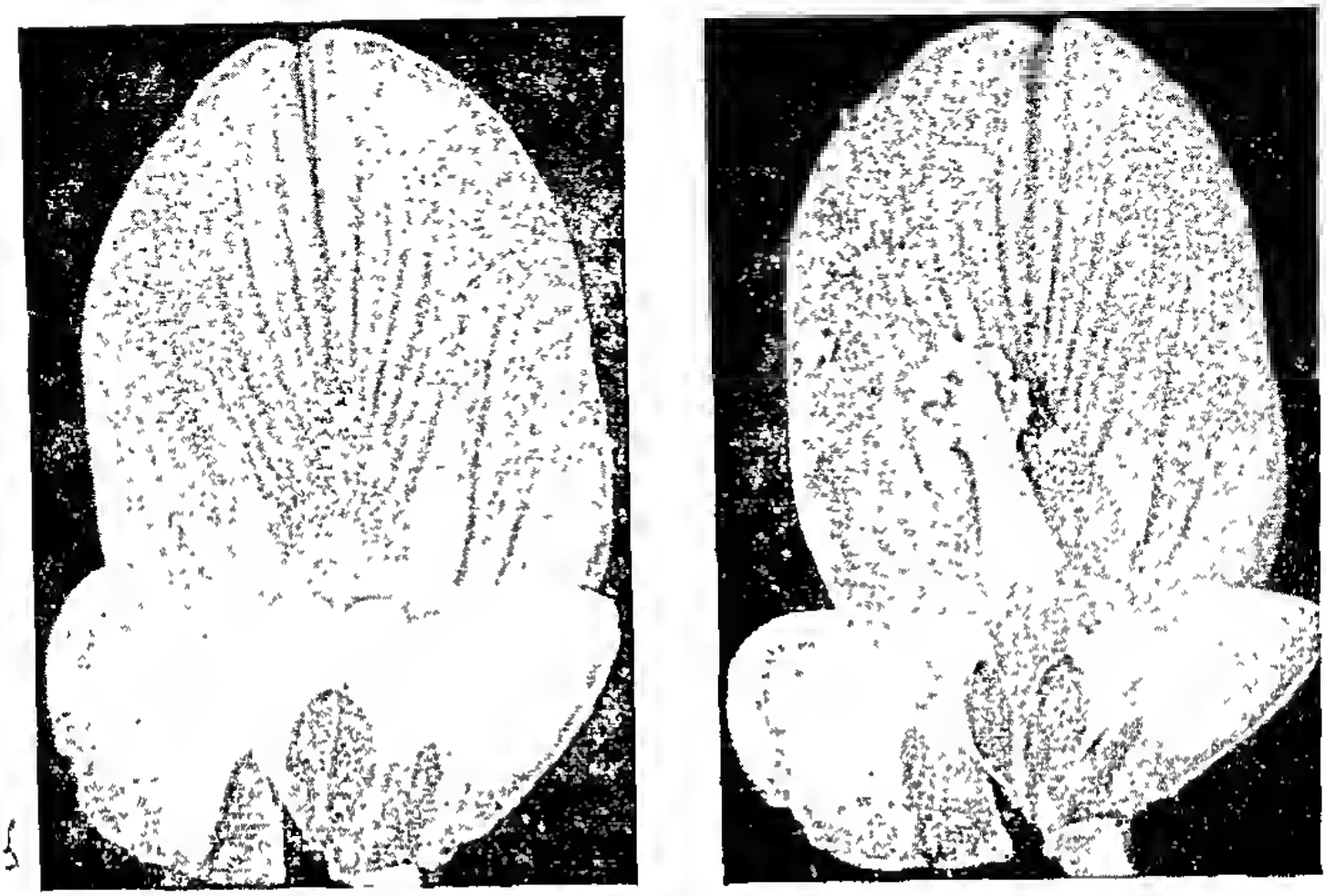


Fig 18 5 Flower structure and pollinating mechanism in lucerne *Medicago sativa* Position of staminal column (pistil and stamens) tripped and untripped

Many common cross pollinated forage legumes are highly self sterile They include various species of *Trifolium Lotus Melilotus* and *Medicago* (lucerne) Red clover *Trifolium pratense*, is almost completely self sterile although occasional plants may set a few seeds after self pollination [63] When red clover is self pollinated the pollen tubes usually traverse about one half the distance of the style at a normal rate after which their growth is so retarded that the pollen tube seldom reaches the embryo sac during the life of the floret In red clover, the pollen tube growth rate is an inherited characteristic which is controlled by a series of sterility alleles [64] When the pollen tube contains the same sterility allele as that in the style growth rate of the pollen tube is retarded to such an extent that it rarely reaches the ovule (Fig 3 17) If the clover plant is cross pollinated by pollen with an allele different from that in the style pollen tube growth is not checked and growth continues at a normal rate until the pollen tube reaches the ovule Many sterility alleles have been identified in different red clover plants from the same population A noninhibiting or self fertility gene is present in some self fertile lines of red clover This permits the self pollen tube to grow at the same rate as the pollen tube from an unrelated plant Similar systems of inherent self and cross incompatibility have been identified in white clover *Trifolium repens* [3] and in alsike clover, *Trifolium hybridum* [66] and probably exist in other species of cross pollinated legumes including those grown in



18.6A 18.6B

Fig. 18 6. Flower of lucerne (*Medicago*). A: Before tripping. B: The same flower after tripping. The staminal column (pistil and stamens) have been released from the keel petals.

tropical areas which have a high degree of self-sterility.

Various techniques are used for the artificial emasculation and cross-pollination of forage legumes.[31] In general the methods fall into two groups in which (*a*) the pollen is transferred to the female plant by hand, or (*b*) the pollen is carried from one plant to another by insects. Clovers may be emasculated by removing the corolla, staminal tube, and all the anthers with a small forceps, but with the pistil left intact.[67] Anthers and pollen are sometimes removed from flowers with suction, or washed off with a jet of water, or killed by immersing the flower in an alcohol solution or hot water. A camel's-hair brush or a small piece of cardboard may be used to transfer the pollen to the stigma. In crops which have a high degree of self-sterility, such as red clover, it may be unnecessary to emas-

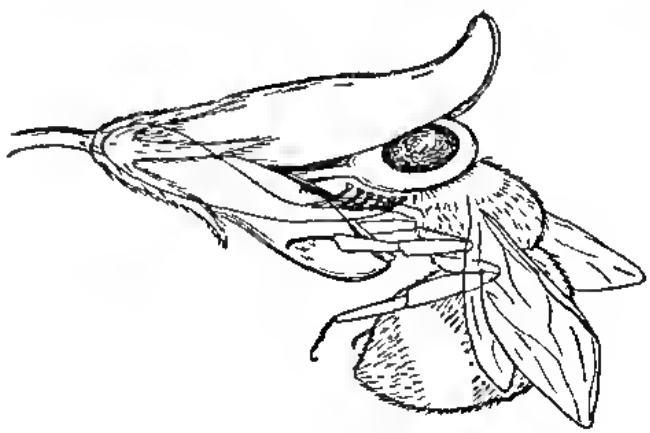


Fig. 18 7. Mechanism by which pollen is deposited on a bee when a flower of lucerne (*Medicago*) is tripped.

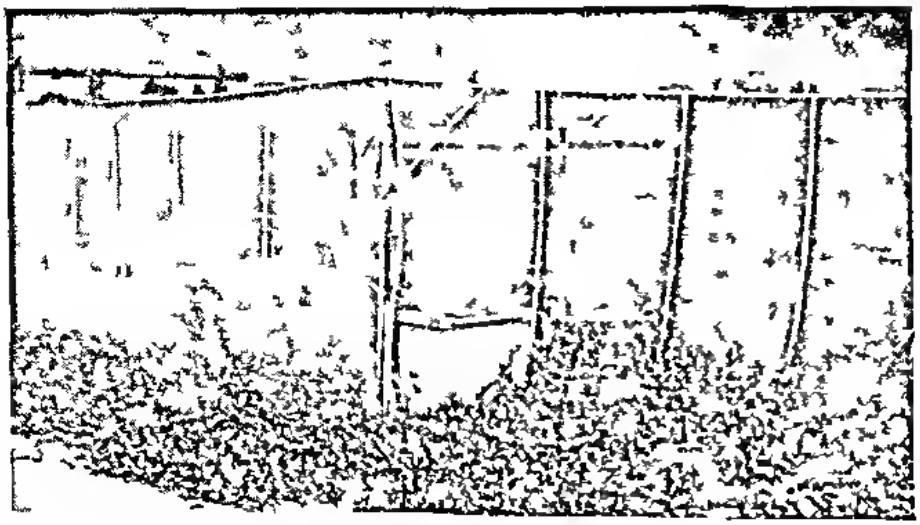


Fig 18 8 Insect proof cage covered with plastic screen wire in which strains of lucerne are being grown in Utah, U S A for controlled pollination studies. A hive of honey bees has been placed inside the cage to facilitate cross pollination of the lucerne

culate especially if one of the parents has a dominant marker gene so that plants originating by self pollination may be identified Plants should be checked for the presence of self fertility genes before eliminating the emasculation procedure entirely Oftentimes selfs can be eliminated because of their reduction in vigour When crossing legumes in a glasshouse all vents should be screened to keep out insect pollinators Cross pollination by bees or other insects is accomplished by growing the two parents in a cage in which bees are present (Fig 18 8) [62] Bees may be cleansed before being placed in a cage by washing them with water since the pollen grains will absorb water causing them to burst Self pollination is accomplished by bagging the flowers to exclude foreign pollen and then tripping or otherwise manipulating the bagged flowers by hand

VEGETATIVE PROPAGATION OF FORAGE CROPS

A group of plants propagated asexually from a single plant is a *clone* Most forage crops lend themselves to asexual propagation by (*a*) stolons (a runner or creeping stem above ground that produces roots) (Fig 18 9A) (*b*) rhizomes (underground stems that develop roots) (Fig 18 9B) (*c*) dividing the crowns or (*d*) stem cuttings (Fig 18 10) Grass plants that spread by stolons or rhizomes are easily divided to obtain vegetative sprigs which may be used to establish clones (Fig 18 11) Legumes such as lucerne or berseem are readily propagated by stem cuttings (Fig 18 10) in moist sand or in slowly moving water at temperatures of 19 to 21 degrees centigrade Rooting may be stimulated by treatment with growth hormones but such treatments are seldom necessary Vegetative propagation is used by the forage breeder to (*a*) establish clones (*b*) evaluate superior plants (*c*) maintain original plants used in strains or (*d*) propagate strains or varieties which are poor seed producers

GENETIC COMPOSITION OF FORAGE CROPS

The genetic composition of forage crops follows the general principles described for the self and cross pollinated species already studied Individual plants of normally self pollinated crops are normally homozygous True breeding lines may be established from selected plants and maintained with comparative ease Plants from normally cross pollinated forage crops are heterozygous For this reason improvement of the cross pollinated species is based on systems of breeding different from those used for the self pollinated species Chromosome irregularities occur in many of the cross pollinated forage crops especially in species with polyploid origin or in apomictic species The apomictic species present special problems to the breeder not common in other species For example with some types of apomixis hybridization between strains would be difficult or impossible

Results of Inbreeding Cross Pollinated Forage Crops Inbreeding cross pollinated forage crops generally results in reduction in (*a*) vigour and (*b*) fertility and seed production [61] The reduction in vigour is comparable to the reduction in size and productiveness obtained from inbreeding open pollinated maize Reduction in forage and

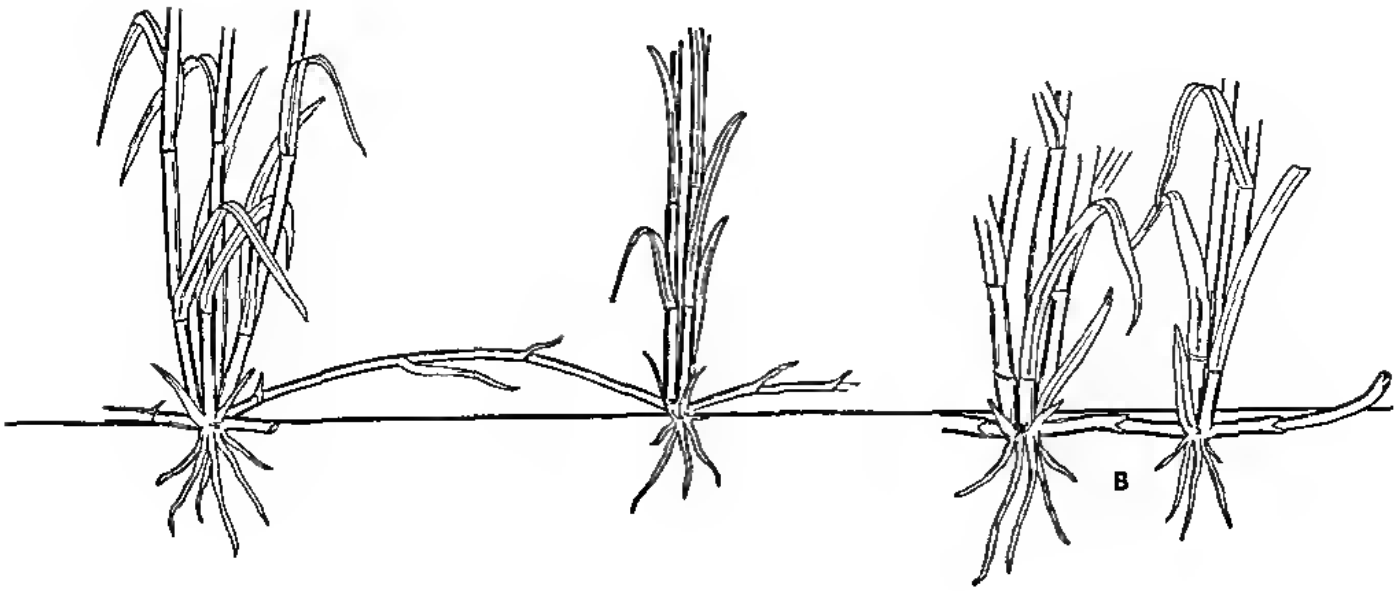


Fig 18 9 Vegetative propagation in grasses A Stolons B Rhizomes

Fig 18 10 Vegetative propagation of lucerne by stem cuttings A Stem cutting before rooting B Development after six weeks C Development after two months D Development after five months

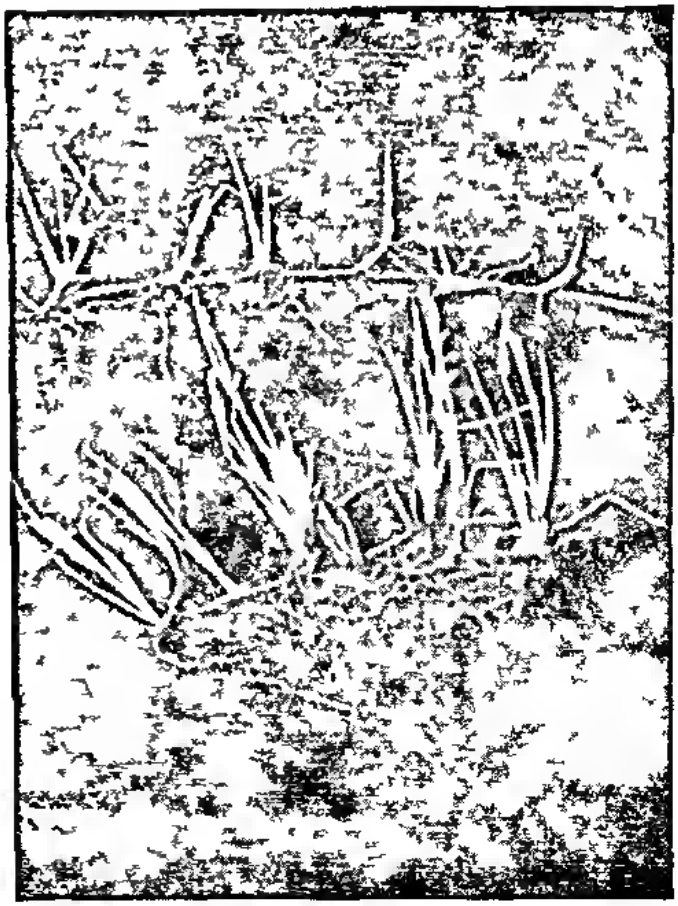


Fig 18 11 Vegetative sprigs may be used to establish clones of grasses

seed yields of lucerne after one to eight generations of inbreeding at the Nebraska Agricultural Experiment Station[58] are presented in Table 18 2

Table 18 2 Yields of Self-Fertilized Lines of Lucerne Expressed as Percent of Three Parental Open Pollinated Varieties, Grimm, Hardistan, and Ladak, Average of Two Years, 1938 39, at Lincoln, Nebraska[a]

Selfed generations	*Lines tested*	*Yield as percent of parents*	
		Forage	*Seed*
1	54	68	62
2	17	48	39
3	9	59	38
4	13	51	36
5	1	41	29
6	—	—	—
7	1	26	15
8	4	28	8

[a] After Tysdal *et al* [41]

Considerable variation in the vigour and fertility after inbreeding exists among different cross pollinated forage species and also among plants within a species [29] The clovers are greatly weakened by inbreeding and lines that set seed freely after successive generations of selfing are extremely rare Grasses on the other hand vary in this respect and plants that show very little reduction in vigour or fertility after inbreeding are found occasionally

NATURAL SELECTION IN FORAGE CROPS

When cross pollinated forage species are grown over a period of years in the same local area the genotypes best adapted to the local conditions tend to survive while the unadapted genotypes tend to be lost from the population [43] This is part of the process of natural selection by which plant species have evolved and become adapted in their native habitats Population types created by natural selection and adapted to a particular habitat are termed *ecotypes* Within a single forage species numerous ecotypes may evolve, each adapted to a local climatic or soil condition or to the system of management under which the crop has been grown Common lucerne grown for several generations in northern U S A is more winter hardy than common lucerne grown for several generations in southern U S A Strains of bromegrass introduced from central Europe and grown in old pastures in central U S A for many years were found to be more tolerant of heat and drought in the seedling stage and earlier in maturity than strains originating from northern Europe or Siberia and grown in the northern states [42] In Great Britain cocksfoot (orchardgrass) from fields that had been heavily grazed for many years produced a dwarf leafy growth which persisted under intensive grazing Cocksfoot plants from adjacent waste areas or areas that had been cut for hay, were tall early and sparsely leafed [53]

Heterogeneous populations of cross pollinated crops with genotypes that are highly heterozygous are differentiated into ecotypes more quickly than self pollinated crops Short lived crops will adapt themselves to changing environments more rapidly than long lived perennials because genetic recombinations occur more frequently The concept of ecotype formation is an important factor influencing the breeding of forage crops Because natural selection is such a powerful force in determining plant adaptation forage plants well adapted to the local environment usually will be found in old meadows or pastures which have been successfully maintained in an area over a period of many years To determine the adaptation of new strains it is necessary that they be tested in the areas where they are to be recommended and with systems of management comparable to those generally used by the farmers in that area Genetic changes that may be induced in a population must be considered in the maintenance of varieties of forage crops otherwise seed produced in another environment for several generations may be different from the strain originally developed [4 50 55]

BREEDING SELF POLLINATED FORAGE CROPS

In breeding self pollinated forage crops selection and hybridization procedures are similar to those employed in the production of new varieties of wheat or rice The breeding methods are based on the assumption that individual plants within a

normally self fertilized population will be homozygous and that relatively true-breeding lines can be developed from superior plants selected from mixed populations or hybrid progenies

Whether or not superior lines can be isolated from a natural population will depend upon the range of variability within the population and the precision with which the breeder can identify the superior genotypes Recombinations of desirable characters are obtained by crossing specific strains and selecting lines with the desired combinations from the segregating progenies Backcrossing may be used to add specific characters to an already adapted variety Blends of varieties may be made to incorporate the multiline concept as opposed to the use of pure lines

Self pollinated forages are mostly annuals In general, they are grown less extensively and have less economic importance than the cross-pollinated species Exceptions are sorghums, bajra, or millets, normally cultivated for their grain but which may also be grown as fodder crops

BREEDING CROSS POLLINATED FORAGE CROPS

In developing breeding procedures for cross pollinated forage crops, observations based on breeding behaviour of many different species have been taken into consideration The more important of these observations are summarized here

1 Cross-pollinated forage crops are highly heterozygous

2 Inbreeding, or close breeding, leads to a depression of vigour and loss of fertility although species and individual plants within a species vary considerably in this respect

3 Individual plants, or lines, may be propagated vegetatively as clones

4 Individual plants, or lines, differ in their ability to combine with other plants, or lines, and produce progenies with superior performance

These facts were not so well known when forage crop breeding was initiated In the beginning it was necessary to accumulate information on the breeding behaviour of each of the different species in order that breeding procedures could be developed intelligently and adapted to particular species Accumulating this information and perfecting techniques occupied much of the breeder's time and diverted efforts that otherwise could have been directed into more productive breeding efforts

Breeding methods for cross pollinated forage crops are discussed under the topics *introduction, selection, synthetic varieties, hybridization,* and *polyploidy* Examples, where available, of varieties developed by each procedure are cited to illustrate the method This is not necessarily an inclusive list of breeding procedures Neither do all forage crop breeders use procedures as specifically outlined here Breeders employ the methods in different ways, depending upon (*a*) the species with which they are working, (*b*) the specific objective which is foremost in their improvement programme, and (*c*) the facilities available

Currently, procedures in forage crop breeding stress the production of 'synthetic varieties' in which seed from superior plants or strains is composited and the variety is then propagated from seed produced for a limited number of generations by open pollination In breeding synthetic varieties it is necessary first to evaluate the combining ability of the plants or lines to be composited

Introduction As has been related with other crops, introduction plays an important role in the initiation of any breeding programme In forage crops few species of high quality forage are native to southern and southeastern Asia, so introduction of new species will be the first consideration Already berseem introduced into India from Egypt in 1904[38] and Napiergrass introduced from tropical Africa[41] are examples of exotic species which have become established forage crops Most improved forage species are grown in the temperate climates of the world and it is doubtful that they can be acclimatized for growing in the tropics Greatest success is most likely to come by the introduction and utilization of species either wild or cultivated from other tropical or subtropical areas

It is known that the greatest diversity of types of a crop will be found in the region where that crop originates[59] For this reason the centre of origin for a crop is a good place to look for new sources of breeding material During the time that a newly introduced grass or legume is becoming established within a new area there may be a shift in the genetic types that predominate within the introduced species The genetic changes within these populations result in the development of biologically stable ecotypes adapted to the new local environment The

greatest shift will occur in the boundaries of the new area of adaptation, for there the introduced species will be struggling for existence [60] The shift in the genetic types within the population is a result of the selection pressure of the new environment which tends to eliminate the genotypes least fit to survive The extent of the change, and thus the chance for survival, will be limited by the possible genetic re combinations within the introduced species

Thus far only the introduction of cross pollinated *species* and the natural development of local ecotypes within them have been discussed The same process of acclimatization accompanies the introduction of a new *strain* or *variety* of a particular species If the strain has been developed and refined in such a way as to reduce the genetic variability the new area of its adaptation may be restricted This means that highly bred varieties such as synthetics derived by combining a small number of individual genotypes, will generally be unadapted in a new area unless introduced into an environment similar to that in which they originated New varieties of forages developed in the plant breeding stations of western Europe, when introduced into the United States, or varieties developed in the U S A and introduced into Europe, almost never performed as well as local ecotypes or selections from local ecotypes of the same species This does not preclude the possibility that occasional varieties with superior specific characteristics such as drought tolerance or disease resistance will be introduced and will fill an important need Introduced strains may contain valuable genes, such as those for disease resistance, which can be incorporated into adapted types even though the introductions themselves may be unproductive or unadapted

Examples are cited here of two varieties of lucerne that were introduced into the United States, one from Europe and one from India These examples illustrate how introduction of forage varieties serve the plant breeder In each example it may be assumed that considerable natural selection and acclimatization took place after the strain was introduced into the U S However, we must further assume that each strain contained a range of genetic variability when introduced, otherwise the acclimatization could not have taken place

Grimm. Lucerne was taken into Carver County, Minnesota, by Wendelin Grimm from near Baden, Germany, in 1857 It was later established that this variety of variegated lucerne, which was called **Grimm,** had extreme winter hardiness The hardiness of Grimm was not generally recognized until about 1900, and it may be assumed that considerable natural selection and acclimatization had occurred by that time

Ladak. Ladak lucerne proved superior to many forms in the northern Great Plains of the U S A and Canada It has superior cold resistance, the capacity for renewing growth after periods of prolonged drought, and considerable resistance to the bacterial wilt disease Ladak was introduced from the plains of northern India about 1910

In India, the Division of Plant Introduction at the Indian Agricultural Research Institute, New Delhi, is systematically introducing and testing new grasses and legumes Over 3,000 herbage strains have been tested of which 136 grasses and 63 legumes are being maintained [46] Promising species are also being tested in the various states for local adaptation [40]

Selection. The effect of natural selection in the development of locally stable ecotypes has already been described This natural selective force is so simple in its application, yet so forceful in its results that no serious consideration should be given to methods for the improvement of a particular forage species that do not utilize the benefits already achieved in nature Local ecotypes relatively stable in type and performance may be found in native forage species or in species introduced sufficiently long ago for them to have become well established in the area of their natural adaptation Excellent genetic strains for the breeding of local varieties may be found in the local ecotypes [65] It is generally very hard to improve upon the best genotypes already existing successfully within a local area except perhaps for specific characteristics, such as disease resistance, when equally desirable genes for such characteristics are not already present within the local population

A MASS SELECTION The simplest selection procedure available to the forage plant breeder is to harvest *en masse* the seed from a locally adapted ecotype This field harvesting procedure has been used to develop numerous strains of forage crops One example from the U S A which illustrates this procedure is Kentucky 31 tall fescue

Kentucky 31 tall fescue. In 1931 tall fescue was observed on a farm in Menifee County, Ken

tucky, where it had been growing since 1887 Seed harvested from the field was increased and later was named Kentucky 31

Harvesting seed *en masse* from an old field does not permit selection of superior types within the field or rejection of inferior plants Neither does it permit progressive improvement from generation to generation except that which occurs from natural selection Furthermore, the mass selection technique is limited to indigenous species, or introduced species which have been grown for a sufficiently long period for a superior genotype to have been evaluated by the natural selection process

Repeated mass selection, as practiced with open-pollinated maize, may also be used with forage crops Seed harvested from superior appearing plants is bulked without control of pollination or regard to progeny performance With open pollinated maize, continuous mass selection for easily identified characters progressively changed the appearance of the maize, with respect to the character being selected, but seldom increased yield We may presume that this principle will apply also to the improvement of cross pollinated species of forage crops, but with the forages the method is not so easily carried out Superior plants are more difficult to identify in a dense population of grasses or legumes than in maize The quantity of seed harvested per individual plant is usually small The perennial nature of many forage species increases the time interval over which a selection programme must continue However, Kenland red clover may be cited as an example where progress in breeding has been made by this procedure In the case of Kenland red clover artificial inoculation with a disease infecting organism was used to increase the selection pressure for disease resistance

Kenland red clover. The Kenland variety of red clover originated from seven locally adapted strains seeded in adjacent beds [21] Seedlings and one-year old plants were artificially inoculated with organisms causing southern anthracnose disease Surviving plants of all strains were harvested for seed, and the seed was bulked to plant the next generation The same procedure was followed for several generations, except that in later years seed was harvested only from three year old plants instead of two-year old plants, and beds were inoculated with organisms causing crown rot The resulting variety, Kenland, has resistance to southern anthracnose and crown rot and stands often persist through the third year

B SINGLE PLANT SELECTION The selection of single plant strains is a common procedure for the development of new varieties of self-pollinated crops, but it is poorly adapted to use with cross-pollinated species Single plant strains of cross pollinated forage crops may be obtained by (*a*) selfing selected plants in successive generations to develop inbred lines as in maize or (*b*) selecting superior open-pollinated plants and permitting self- or sib-pollination within the lines in succeeding generations Closely bred lines are generally reduced in vigour and fertility With them, some system of outcrossing must be practiced to restore forage and seed yields Inbreeding for a limited number of generations is often employed to fix certain desirable characters of a plant selection in a homozygous form, after which the line is maintained as a clone and used in crosses or in synthetics

Development of varieties by increasing the open-pollinated progeny of single plants is generally considered a hazardous breeding procedure with cross pollinated forage species due to the narrow genetic base upon which the variety would be established However, an outstanding variety of lucerne has been developed successfully by this procedure

Buffalo. Buffalo was developed at the Kansas Agricultural Experiment Station from the progeny of a single open-pollinated plant selected in 1929 for wilt resistance [16] The initial selection was followed by several years of close breeding and rigid selection for wilt resistance

In species which may be propagated commercially by vegetative sprigs, such as the stoloniferous grasses, it is possible to form a new variety from a single, superior plant The Coastal variety of bermudagrass was increased asexually from a single F_1 hybrid plant from a cross between Tift bermudagrass and an introduction into the U S A from Africa [8] It is propagated entirely from vegetative sprigs Also, single plant selections may be used to establish clones which are then combined to form synthetic varieties Some form of a progeny test is used to determine which plants are to be combined into the synthetic

C RECURRENT SELECTION Recurrent selection may be used to concentrate genes for desirable characteristics in a forage crop as in populations of other

cross pollinated crops With recurrent selection, selected plants or clones are crossed in all possible combinations The hybrid plants resulting from these crosses are composited and increased in isolation to establish a bulk population from which a new selection cycle can be started (Fig 4 5) The recurrent selection principle may be employed also in conjunction with other breeding systems in the improvement of forage crops For example, superior plant populations resulting from mass selection procedures may be the basis for starting a new selection cycle Superior single plant strains, or inbreds, selected for a particular characteristic, may be crossed and the hybrids used to start a new selection cycle The recurrent selection procedure *may be used after the development of synthetics as* a source of new breeding materials

The effectiveness of recurrent selection has been demonstrated with sweetclover [27] Mean yield of a population of Madrid sweetclover plants averaged 91 percent of the Madrid check Mean yield after the first cycle recurrent selection was increased to 121 percent of the check, and to 152 percent of the check with the second cycle recurrent selection

Synthetic Varieties. Synthetic varieties of forage crops may be developed by combining either strains or individual plants into a composite strain This is a commonly used procedure in forage crop breeding The method of combining individual plants into a synthetic variety originated at the University College of Wales, located at Aberystwyth, and was originally described by Dr T J Jenkin in 1931 [22]

A MULTIPLE STRAIN VARIETIES A synthetic variety of forage crops may be synthesized by blending seed of two or more individual strains The synthetic variety produced is increased by open pollination The original strains entering into a synthetic are commonly maintained separately so that the variety may be reconstituted at any time When the synthetic is reconstituted, strains are composited in the same proportions as used in the original synthetic, or the composition of the synthetic may be changed by altering the proportions of the strains, by adding new strains, or by substituting a new strain for one used previously Example of a multiple strain variety developed in the U S A is Ranger lucerne

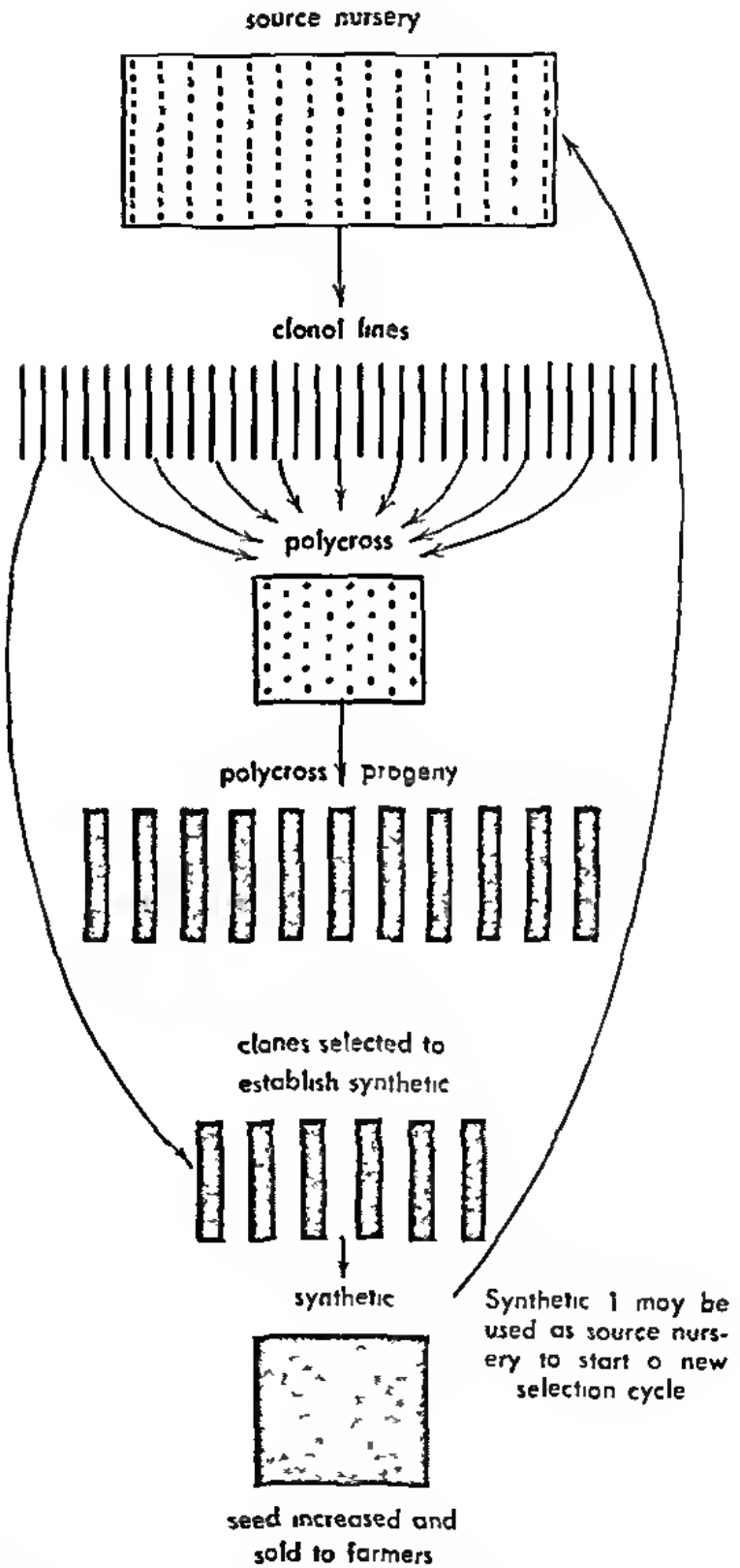
Ranger lucerne was synthesized by blending seed of five strains[56] as follows

45% from a strain of Cossack
45% from three strains of Turkistan
10% from a strain of Ladak

The strains originated as wilt resistant inbred lines, each of which was outcrossed with other lines and then increased in isolation Ranger is wilt resistant, but is variable in plant type and flower colour The original strains used in producing Ranger were not maintained so the Ranger variety cannot be resynthesized In this connection it is now performing as a mass selection

B MULTIPLE CLONE VARIETIES A synthetic variety of forage crops may be developed by combining individual clones [14 17,22 23 54 58] First, large numbers of plants are screened for superior characteristics and established as clones Superior clones, selected *on the basis of phenotype, are then crossed and the* progeny is tested by various procedures to determine its combining ability On the basis of the progeny *performance, final choice of clones* entering into the synthetic variety is made Seed from the clones chosen is mixed to produce the synthetic, which is then increased for a limited number of generations by open pollination The original clones entering into the synthetic are maintained so that the variety can be reconstituted at regular intervals Also, the synthetic may be improved by the addition or substitution of new clones The exact procedures used will vary with different breeders but the basic step in developing a multiclone synthetic is illustrated in Fig 18 12

Regardless of the species being improved, it is necessary to start with a large group of plant selections to ensure a sufficient range of genetic variability Vigorous and productive clones are desired that can be easily maintained and that will have vigorous and productive progenies when tested for combining ability Several thousand plants may be selected for the source nursery *(Fig 18 13)* By visual inspection, 200 to 400 of the superior plants are chosen and clonal lines are established by asexual propagation The original plant selections may come from old established pastures or meadows, introductions, hybrid populations, or other sources The clones are screened to find vigorous lines with special characteristics, depending upon the species and the specific objectives Subjection of clonal lines to adversities, such as severe clipping disease epidemics, or cold tests, will aid in identifying clones with superior qualities Inbreeding and selection within the clones may be used to fix



SOURCE NURSERY
Several thousand plants are assembled from many sources Superior plants may be inbred one or more generations to fix desirable characters

CLONAL LINES
Established from 200 to 400 superior plants

POLYCROSS
Twenty-five to fifty superior clones are grown in an isolated nursery and random cross pollination between clones permitted. Seed is harvested and bulked by clones

POLYCROSS PROGENY TEST
Seed from polycross grown in performance tests Clones are evaluated on basis of polycross progeny performance

ESTABLISHING SYNTHETIC
On the basis of the polycross progeny performance, 4 to 10 of the original clones are selected to establish a synthetic Clones are isolated and random interpollination is permitted

INCREASING SEED OF NEW SYNTHETIC
Equal quantities of seed are harvested from each clone and bulked to grow synthetic 1 generation Open pollinated seed is harvested to grow synthetic 2 and succeeding generations of new variety.

Fig 18 12. Basic procedure for developing a multiclone synthetic

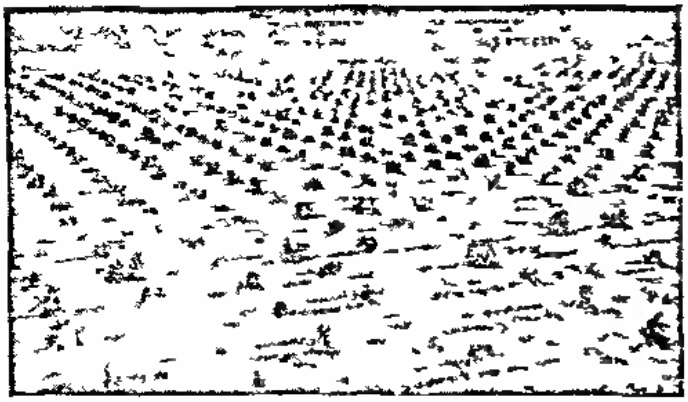


Fig 18 13 A source nursery of individually spaced plants of blue gramagrass growing in the U S A Note the comparative vigour of the different plants Some plants were too weak to survive and were lost

desirable characteristics in the homozygous form Twenty five to fifty of the superior clones, as determined by visual evaluation, are then chosen for further testing

Next, the combining ability of the individual clones is compared In principle, this step is comparable to determining the general and specific combining ability of maize inbreds in the development of single and double cross hybrids Different procedures may be used [6 52 52] Clones may be chosen for synthetic combinations on the basis of the performance of one or more of the following (*a*) open pollinated progenies, (*b*) inbred progenies, (*c*) polycross progenies, (*d*) single cross progenies, (*e*) topcross progenies Of these procedures, polycross performance is used most widely for determining preliminary combining ability of clonal lines

The *polycross test* is a method whereby clonal lines in an isolated group are interpollinated by natural means and the outcross progenies of each clone are tested The essentials of the polycross test are as follows

1 Twenty five to fifty clones are chosen and grown in an isolated plot The clones are replicated in such a fashion that each plant will be fertilized with a random sample of pollen

2 Seed is harvested from each plant in each replicate and bulked by clones

3 Open pollinated seed from each clone is planted in a progeny test for evaluation of yield and other characters

4 Four to ten, or more, clones with superior combining ability, as measured by progency performance, are chosen to produce a synthetic, or to start a recurrent selection cycle

The polycross method of testing progeny performance is in some respects similar to the topcross method of testing inbred lines of maize for general combining ability [57 58]

Information on the specific combining ability of the clones may be obtained, if desired, by single cross tests Ten or more original clones with superior polycross progenies are single crossed in all possible combinations (also called *diallel* crossing) The performance of the single cross progenies is tested to determine specific combining ability of the clones Making and testing single crosses is a refinement in technique that is not used by all breeders This step requires considerable time to make the necessary single crosses if the number of clones to be tested is very large Single and double crosses may be used in the development of hybrid varieties as will be discussed later

Four to ten of the original clones with superior combining ability, on the basis of polycross and single cross tests, are chosen to make up the synthetic Equal amounts of seed from each clone are mixed and the bulk is planted in isolation The synthetic variety may be increased by open pollination for a limited number of generations The original clones entering into the synthetic are maintained, and the variety reconstituted at regular intervals New clones may be added, or substituted for existing clones, at any time to improve the performance of the synthetic

The aim of this method of breeding is to establish a variety with a sufficiently wide range of genotypes to maintain vigour, yet approaching homozygosity for the particular characteristics used as the basis for selection [21 51] For example, all the plants entering into a synthetic variety of some pasture grass might vary markedly in genotypes for plant growth and vigour, yet be relatively pure for resistance to a specific disease The number of clones that may enter into a synthetic variety is still a matter of speculation From four to ten are often suggested Too few clones may result in a narrow genetic base and a narrow range of adaptation for the synthetic variety, yet increasing the number of clones to give greater genetic variability and wider adaptation for the synthetic may result in poorer performance for a specific area of adaptation [15] Generally, much variability in some charac-

teristics is still contained in a synthetic variety of forage crops derived from a very small number of clones

The development of multiple clone synthetics has been carried out extensively at the Welsh Plant Breeding Station, Aberystwyth, where many synthetic forage crop varieties are now in commercial use [25] There, three strains each of ryegrass timothy, and orchardgrass have been developed One strain of each species is a tall, leafy hay type, one strain of each is a low growing, persistent pasture type, and the third strain is a dual hay pasture type The synthetics are reconstituted regularly from the original clones The synthetics may be improved at any time by adding or deleting a specific clone, or by substitution of a new clone for one originally present in the synthetic

Example of a multiple clone variety is Vernal lucerne

Vernal. Vernal is a synthetic variety with a broad genetic base Fifty percent of the germ plasm comes from six Cossack plants originating from surviving plants in an old Wisconsin field, the remaining germ plasm comes from five F_2 plants from a cross between cultivated alfalfa, *Medicago media*, and wild yellow flowered alfalfa, *M falcata*

Hybridization Hybridization may be practical to increase genetic recombination Artificial or controlled hybridization may be used in forage crop breeding in several ways These include (*a*) the crossing of ecotypes or species to supplement natural variation, (*b*) the addition of specific features to an established variety by backcrossing Crossing to increase the range of genetic variability within a population is a common plant breeding procedure When local ecotypes do not contain sufficient variation to permit selection for desired characters, the natural variation may be supplemented by controlled crosses with other local ecotypes, with introductions, or with closely related species If it is desired to add particular characteristics to a well established variety, the backcross programme of breeding may be used For a successful backcross programme it is desirable to have (*a*) a well adapted variety, (*b*) a suitable source of disease resistance or other character to be added, which is simply inherited, and (*c*) suitable techniques for identifying characters being added

Hybrid Forages. The successful utilization of heterosis in the breeding of maize, sorghum, and other crops has prompted forage breeders to attempt the utilization of heterosis in the breeding of forages The proposals have included *varietal crosses*, production of *2 clone synthetics*, utilization of *single crosses to produce F_1 seed*, and *vegetative propagation of F_1 plants*

Making *varietal crosses* is perhaps the simplest procedure Seeds of two varieties are mixed and the harvested seed planted Presumably interpollination between the varieties would result in some heterosis and increased yield Variety crosses of lucerne at the Iowa Agricultural Experiment Station, in general, did not give yields significantly above the mean of the two parent varieties [68]

A more refined procedure would be the production of a *two clone synthetic* in which clones were selected for maximum specific combining ability If the clones possessed a high degree of self sterility most of the seed in the first generation would result from interpollination between the clones While significant gains in yield have been obtained from two clone lucerne synthetics, problems in pollination have arisen It has been established that bees may work on only one clone in the combination resulting in self pollination and subsequent loss in vigour [18] A similar procedure is used successfully in the U S A with bajra, a wind pollinated fodder plant Two inbred lines of bajra are interplanted Seed harvested from bajra, a largely cross pollinated crop, would normally be 70 percent cross pollinated and 30 percent self- or sib pollinated When planted the cross pollinated seed will produce plants with greater seedling vigour which will suppress the growth of the selfed or sibbed seed so that more than 70 percent of the adult plants will be F_1's Hybrid pearl millet (bajra) produced in this manner in the U S A yielded as much as 100 percent more forage than the best open pollinated variety available

A procedure for producing F_1 *hybrid seed* in lucerne was described as early as 1942 [58] As proposed for lucerne the method involves

1 Finding combinations of relatively self-sterile lines that produce high single cross yields

2 Establishing two single cross seed production fields by vegetative propagation

3 Obtaining single cross seed by forced cross-pollination (between self sterile lines)

4 Mixing seed of two single crosses to plant a double cross seed production field.

While the above procedure presents an attractive possibility, its application is dependent upon the successful production of seed at a reasonable cost, and upon obtaining hybrids that will yield sufficiently above synthetics, or varieties produced by other means, to warrant the extra expense in their production Apparently difficulties in pollination and seed production have not been overcome since no hybrids of lucerne are currently being produced by this procedure

Hybrid F_1 plants have been used to establish varieties of grasses which are propagated by vegetative means In the U S A the Coastal variety of Bermudagrass (*Cynodon dactylon*) was increased vegetatively from an F_1 hybrid plant from a cross between Tift Bermuda and an introduction from South Africa In India, Pusa Giant Napiergrass, was developed by crossing Napier or elephant grass, *Pennisetum purpureum*, introduced from Africa, with cultivated bajra, *Pennisetum typhoides* (Fig 18 14) [44] Being an interspecific hybrid between Napiergrass ($2n = 28$) and bajra ($2n = 14$), the F_1 has 21 chromosomes and is sterile Propagation is by stem cuttings or rooted slips

Polyploidy. Polyploid forms of a crop, as a consequence of their larger cell size, often represent giant types when compared with related diploids [2] Because polyploids are reduced in fertility and do not set seed freely, it is generally believed that polyploidy would be a more productive method for breeding forage and root crops, where the increase in plant size could be utilized, than for the breeding of grain crops Promising results with artificially induced tetraploids in forage crops have been reported from Europe in red clover and alsike clover (Fig 18 15) [30,33] These two species have relatively low chromosome numbers (red clover, $2n = 14$, alsike clover, $2n = 16$), and are cross fertilized Original tetraploid plants, obtained from doubling chromosomes in diploid clover plants, are usually quite variable and are generally inferior to the diploids, especially in seed setting ability It has been found necessary to double the chromosome number in a very large amount of material and then practice intensive selection and breeding among the tetraploids [37] Treating seedlings with 0 2 percent colchicine has proved to be the best method of inducing autoploidy [13,49] Poor fertility and seed setting has been a serious weakness of the tetraploid strains, but improvement in seed-

Fig 18 14 Pusa Giant Napiergrass developed at the Indian Agricultural Research Institute by crossing Napiergrass (*Pennisetum purpureum*, $2n=28$) with bajra (*P typhoides*, $2n=14$) and propagating the sterile F_1 hybrid by vegetative means

setting ability has been obtained by selection Perhaps one reason for the difficulties in utilizing artificial autoploids directly in breeding new varieties is that most forage species are already polyploids As such they already are at or near the maximum chromosome number for optimum development [17] Another consequence of naturally occurring polyploidy in the forage species is that it increases the complexity of genetic ratios However, the polyploid species will tolerate to a greater extent deficiencies in chromosomal material than will diploid species

In India a new colchicine induced polyploid variety of berseem, Pusa Giant Berseem, has been released for cultivation [38] The chromosome number of four diploid varieties of berseem ($2n = 16$) was doubled by treating young seedlings with colchicine Over 1100 tetraploid ($2n = 32$) seedlings were produced The best selections were found to be equal to the diploid parent material in dry matter per hectare, more leafy than the diploid, but reduced in seed setting [10,36]

OBJECTIVES IN BREEDING FORAGE CROPS

Objectives in breeding forage crops vary with the species, the region of production, and the utilization of the crop for fodder, pasture, or other

purposes Since there are so many forage crops, it is impossible to enumerate a group of objectives which will apply with equal importance to all species Ultimately, it is necessary to study each species individually and to consider the objectives that are peculiar to each as determined by the nature of the species, the area where it is grown, and its manner of utilization However, there are a few broad objectives that apply to many species[1 17 60] which will be considered here

Yield. High forage and high seed yield are not usually compatible traits Strains selected for high forage yield frequently are poor seed producers, or strains selected for high seed yield are poor forage producers This may be illustrated by results secured at the Nebraska Agricultural Experiment Station with F_1 lucerne hybrids (Table 18 3) As a result, it is sometimes necessary to compromise between high forage yields and satisfactory seed yields in determining which strain to increase

Table 18.3. Forage and Seed Yields of F_1 Single Cross Hybrids of Lucerne Compared with Hardistan, Ladak, and Grimm Check Varieties[a]

	Yield per plant (gm)		*Yield as percent of checks*	
	Forage	*Seed*	*Forage*	*Seed*
3 check varieties	1289	10 25	100	100
28 F_1 hybrids	1235	9 94	96	97
top 10 hybrids in forage yield	1480	5 30	115	52
top 10 hybrids in seed yield	1060	17 29	82	169

[a] Adapted from Tysdal *et al* [35]

A FORAGE YIELD Good forage production is an essential characteristic in any improved forage variety The type of plant which will produce a satisfactory yield of forage will depend upon the particular species and how it is to be utilized Many grasses and legumes are grown in mixtures and yields under competitive conditions are important in those species At the Welsh Plant Breeding Station, which pioneered in grass breeding studies,

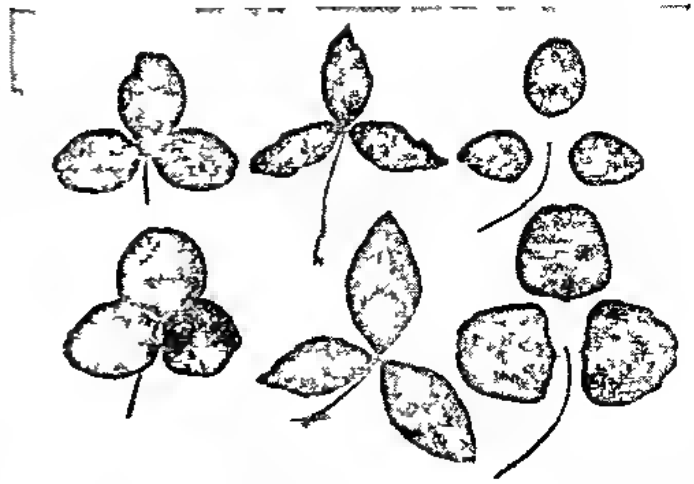


Fig 18 15 Leaves of diploid (top) and tetraploid (bottom) red clover (*Trifol um pratense*) Note the larger size of the leaves from tetraploid plants

the plan has been to develop separate varieties for hay and for pasture in important species such as timothy, cocksfoot (orchardgrass), and ryegrass Low growing leafy plants that have persisted under close grazing are selected as a basis for the pasture type varieties Vigorous tall growing plants that set seed freely are selected for the hay type varieties

Quick recovery after the crop has been grazed off or cut for hay is needed to obtain maximum forage yields Development of strains with better seasonal distribution of forage growth would extend the use of certain species at times when they now become more or less dormant Forage yields may be increased by breeding for resistance to disease insects drought, heat cold, and competitive ability with weeds and other forage species Special techniques are required to evaluate comparative forage yields of different species or varieties [39] These may utilize either clipping, so that weights of forage produced may be compared, or grazing, in which case the gain in animal weight or the yield of milk produced, is used to indicate the comparative forage yields of the species or varieties being tested

B SEED YIELD More rapid progress can usually be made in the increase and distribution of a new forage variety if it produces seed abundantly It has been pointed out that strains with excellent forage production are often poor seed producers In such cases it may be necessary to sacrifice some forage yield in order to obtain satisfactory seed yield, usually a good balance between the charac-

ters is desirable Breeding for high seed production may involve selection for different characteristics according to the species with which one is working Examples of such characteristics are early ripening to escape drought, heat, or frost, adaptation to day length in the area where the variety is to be grown, nonshattering, and greater self fertility A high degree of self fertility is not always desirable in cross pollinated species since the inbreeding may lead to a reduction in vigour

Greater Seedling Vigour. A common reason for failure to obtain satisfactory stands of a new seedling of a forage grass or legume is the inability of the seedling plant to become established quickly so that it may survive unfavourable environmental conditions, such as heat, drought, cold, insects, or compete with weeds or other crop species with which it may be associated Development of strains with greater seedling vigour would increase the ability of the seedling plant to cope with these adverse growth conditions This characteristic is particularly desirable if a species is moved out of its area of optimum environment into marginal production areas Also, it is an important consideration in the breeding of grasses for dry areas, for there favourable weather conditions in which a new seedling may become established are frequently of short duration Studies with crested wheatgrass[19] have demonstrated that seedling vigour is related to seed size and may be increased by selecting for larger seeds

Persistence of Stands. The persistence or longevity of stands of forage crops is essential in long lived species where the maintenance of a dense stand or turf of long duration is desirable, or where frequent reseeding may be expensive and inconvenient The lack of persistence in perennial species may result from many causes Stands may be reduced by disease (Fig 18 16), insects, drought, high temperature, cold, unfavourable soil conditions, or excessive defoliation from cutting or grazing Breeding for resistance to these pests or adverse environmental conditions will result in the development of more persistent varieties Lucerne does not persist well under grazing Creeping rooted types of lucerne have been developed in Canada for use with heavy grazing [19] It is necessary for the breeder to analyze carefully the cause of stand failures for a particular species in each area and then to concentrate on the development of varieties that will persist under

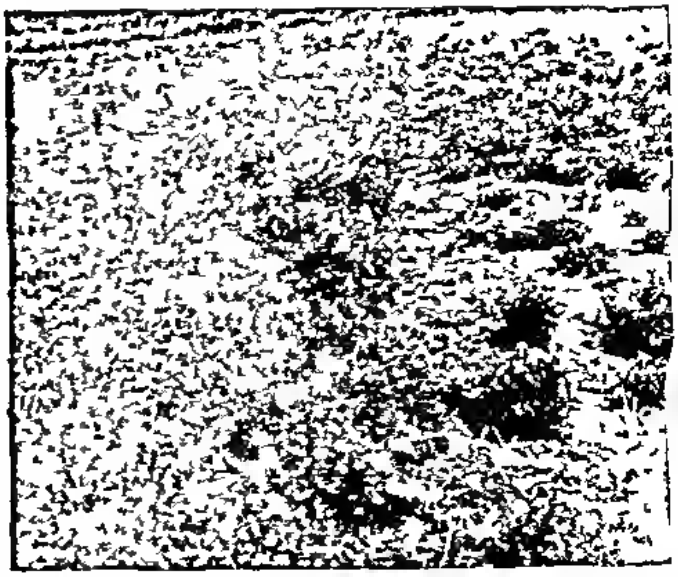


Fig 18 16 Comparative survival in a five-year-old stand of wilt resistant Ranger and wilt susceptible Grimm varieties of lucerne growing in the U S A

the specific conditions responsible for the deterioration of the stands It should be recognized that persistence in many cases may be increased more easily by methods other than breeding, such as the addition of fertilizers to correct extreme soil deficiencies or the adjustment of management practices to eliminate overgrazing But many cases of stand failure cannot be removed by such methods, and it is desirable then to breed for tolerance to the condition responsible The causes of stand failure in a tropical climate may be much different from those in a temperate climate

Disease and Insect Resistance. Increased attention is being given to the breeding of disease-resistant strains of forage species This partly reflects the increased efforts being directed toward all phases of forage crop breeding, but perhaps to a greater extent it reflects a fuller realization of the losses caused by disease and insects in the forage species

A few diseases that reduce stands of certain forage crops have already been cited Diseases and insects may also reduce forage yields, reduce seed yield, and reduce quality of the forage The effect on the quality may be quite pronounced in the case of leaf spotting diseases, or insects such as aphids and leaf-hoppers which attack and cause yellowing of considerable leaf area As forage crop breeding develops in southeastern Asia it will be necessary to evaluate breeding materials for

resistance to the diseases common to the particular species with which the breeder is working

Progress has been made in the U S A in breeding lucerne and vetch for resistance to leaf-hoppers and aphids The Lahontan variety of lucerne is resistant to the spotted alfalfa aphid The spotted alfalfa aphid spread rapidly over states in the southwestern one-quarter of the United States and caused great damage to lucerne stands before resistant strains were developed

Forage Quality. Strains improved in forage quality may be developed by breeding for (*a*) greater nutritive value, (*b*) increased palatability, or (*c*) lower content of toxic substances In addition to genetic variations between species or strains, quality may be influenced by soil, weather, management of the crop, stage of maturity, method of utilization, and disease or insect damage Therefore, it is extremely important that strains being compared for quality be produced under uniform conditions and harvested at a similar state of maturity

The results of numerous studies indicate that forage quality may be improved by breeding [31] The nutritional value of forage may be improved by selection of strains with increased concentrations of the proteins, minerals, and vitamins which are important in feeding value However, the increase in one vital component must not be accompanied by a decrease in another, otherwise the over all nutritional value of the forage may not be increased Leaves are higher in protein, calcium, carotene, and lower in fibre than the stems Breeding for a higher proportion of leafiness is therefore a direct way of increasing the nutritional value of the forage Disease and insect damage may reduce the yield of forage and also the feeding value of forage

Increasing the palatability of certain species, has received the attention of many forage crop breeders The difficulty is that no one seems to know exactly what makes a species or strain palatable It has been suggested that succulence is an important factor in palatability [12] Leafy strains are more palatable than strains with a low ratio of leaves to stems The degree of harshness and hairiness of the leaves and stems may affect the palatability of the species

One of the objections to sudangrass for pasture is that under certain environmental conditions it may develop cyanogenetic glucosides which cause hydrocyanic acid poisoning in livestock Strains of sudangrass growing under uniform conditions may differ in the amount of glucosides they contain Strains have been selected in which the content of glucosides is low, and thereby the danger of hydrocyanic acid poisoning is reduced [20] Attention has also been given by some breeders to the development of strains of sweetclover with a low level of coumarin, an organic compound that reduces the palatability of the sweetclover plant

In breeding for improved forage quality it is necessary that the breeder have means for measuring accurately the differences in quality of the strains he wishes to compare Although it is possible to measure the chemical composition of a strain or the amount of glucoside in sudangrass, it is not always so easy to develop procedures and techniques for comparing the actual feeding value or palatability of strains when consumed by various classes of livestock Such comparisons often require extensive grazing or feeding trials which may occupy considerable land area and are expensive to conduct

SEED INCREASE OF NEW VARIETIES

After new varieties of forage crops are developed, seed must be produced in quantities sufficient to be readily available to the cultivator at a reasonable price Otherwise, he will not grow the improved strains Failure to produce the needed supplies of seed has limited the use of many new forage varieties in the U S A and other countries It is more difficult to increase rapidly seed supplies of a new variety of a forage crop than of a new variety of a grain crop Many forage species are poor seed producers, and this characteristic must be given consideration in their breeding

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19

Seed Production Practices

The primary purpose in plant breeding is to develop better varieties To this end extensive breeding programmes are carried out with all major field crops, the expense being borne by public or by private means, or by the joined efforts of both The cost of this research is justified from the increased returns which the cultivators obtain through the use of the improved varieties The cultivators receive the returns as a result of the increased production and superior quality of the crop grown from the new varieties as compared to inferior varieties Before the potential benefits from an improved variety can be realized, the variety must be distributed widely, and sufficient seed must be produced and made available so that the variety can be grown on the farms in the areas to which it is adapted Otherwise much of the breeder's work would go for naught

To facilitate the systematic increase and rapid distribution of new improved varieties, fairly extensive and well defined seed production practices have been developed in western Europe, the U S A , and in other areas of the world Usually the development of seed production practices has moved forward with the development in breeding This is logical since progress in breeding and the release of new varieties has necessitated the development and organization of mechanics for distribution of the varieties and for maintenance of pure seed stocks after the varieties were released

The situation is essentially not different in India As long as varieties are developed and released for state or local areas only, no elaborate machinery for release or for maintenance of seed stocks of the new variety is required This work could be handled by the State Agriculture Departments With the development of 'All India" coordinated breeding programmes, as in maize, sorghum, millets, and other crops, and the release of varieties with wide adaptation, single states are no longer able to handle all of these functions and a broader, coordinated programme becomes necessary With hybrid crops like maize and sorghum, seed stocks must be maintained and inbred and single cross seed must be produced new each year in quantities to meet the cultivator's needs if the hybrid is to be widely grown and benefits from growing the hybrid are to be realized

In the development of seed production practices it is generally assumed that development of the variety is the primary function of the breeder and that the increase and distribution of the seed is the function of a seed production organization with special facilities and trained personnel to do its particular job (Fig 19 1) The seed production organization may be a branch of a state department of agriculture in India where the variety has been developed by the state research organization, a national seed organization in India if the variety was developed by an "All India" or a coordinated southeast Asia breeding programme, a combination of public and private seed producers as with the seed certification organizations in the United States and Canada, or a private seed organization where the variety has been developed by the plant breeding department of a private seed company Much of the breeding and seed distribution is handled by the private seed companies in western Europe and the U S A

WHO DOES PLANT BREEDING

Plant breeding may be conducted both by public and by private resources In India and other countries of southern and southeastern Asia, plant breeding is done almost wholly by public means, in plant breeding institutes supported by the central government, or in state breeding programmes

Fig 19 1 A seed certification inspector examines a field of wheat in the Delhi area for purity of variety

supported by the state departments of agriculture or the new state agricultural universities In the U S A plant breeding is supported both by public and private means Early plant breeding there was mostly the work of the state agricultural experiment stations operated by the land grant universities and the United States Department of Agriculture, but in recent years private industry has assumed an increasing part of the total breeding programme In crops where hybrid seed is sold, like hybrid maize or hybrid sorghum, or in vegetable crops, a major portion of the breeding and the seed production and seed distribution is handled by private industry This is logical since seed companies can finance breeding programmes only in relation to the income received from the sales of seed Since hybrid seed must be purchased new each year, seed sales are large with these crops and income from sales of seed permit the financing of large breeding programmes In self pollinated crops in which seed sales are relatively small after the initial distribution of a new variety has been made, breeding has been mainly by public agencies, although increased efforts by private agencies are

being made in wheat, soybeans, and fodder legumes In western Europe both public and private breeding work is conducted

HOW A NEW VARIETY REACHES THE CULTIVATOR

Before a new variety is increased, released and distributed to the cultivator its superiority must be proven This is done by growing and testing it thoroughly in the area where it originated and from which it is being distributed Variety yield tests should be carefully conducted and observations accurately recorded The testing procedures should follow recognized field plot technique with adequate replication and a recognized experimental design which will permit statistical analysis of the data Standard varieties should be included for comparison with the experimental strains Yield tests should be conducted by the breeder in cooperation with pathologists and entomologists so that the experimental strains may be screened for disease and insect resistance Tests should be conducted at high fertility levels since crop production demands in the future require that a high level of fertilization be used at all times Testing and developing varieties for low fertility levels simply contribute in the perpetuation of poor cultural practices, procedures which neither the breeder nor the cultivator can afford

Through regional cooperation, yield tests may be conducted over an area of several states In India, the all-India coordinated improvement programmes are in progress with maize, sorghum, millets, wheat, rice and other crops A breeder who has a superior new variety of wheat or rice, or a new sorghum hybrid, may include it in regional or all-India cooperative nurseries Such tests may be grown at 20 to 50 locations throughout India mostly by breeders in the state departments or agricultural universities The yield results, observations on disease resistance, lodging, and other characteristics from all of these nurseries are then available to the breeder to help in the decision as to whether a particular strain should be released for cultivation The regional tests provide the breeder in other states advance information on a new strain before it is released The regional tests also facilitate exchange of new strains or other breeding materials between breeders in the different states

Variety Release Procedures. After a new strain has proven its superiority in local and regional trials it may be named and released as a variety and distributed for cultivation Before a strain is released as a variety it is usually required that it be distinctly superior in at least one characteristic—yield, lodging, disease resistance, or other—over existing varieties available for cultivation Once the decision for release has been made, the new strain must be named and a preliminary seed increase be made Many states in India now have variety release committees that approve the release of new varieties within the state The originating institution supplies the information regarding the new variety including results from regional trials if available, to the state variety release committee, who then makes a decision regarding release of the variety for cultivation within the state An all India variety release committee has also been formulated within the Indian Council of Agricultural Research to approve release on a national basis of maize hybrids, sorghum hybrids and varieties or hybrids of other crops developed in the all-India coordinated breeding programmes or variety releases submitted to them by the states It may be expected that details of these procedures will change from year to year as experience and information on the best procedure is acquired

Maintenance of Breeders Seed. It is generally the function of the institution developing a new variety to maintain *breeders seed* of new varieties originating from that institution *Breeders seed* is the original seed produced by the originating institution and maintained by them as a source for further seed increases If the crop or crop variety is asexually propagated as in sugarcane, the clone is maintained by vegetative propagations In synthetic varieties stocks of the original strains composited are maintained so that the synthetic may be reconstituted, or in the case of hybrids the inbred lines are maintained

In the maintenance of breeders seed it is essential that the genetic composition of the variety is not changed Care must be taken with self pollinated crops to prevent outcrossing and to prevent mixing in threshing or other operations Rogues, mutations and other mixtures that creep in may be rogued out In self-pollinated crops like wheat or rice, several hundred spike or panicle selections may be made and planted in progeny rows the following season An off type row is

and seed harvested and bulked from the remaining rows Inbreds of maize or sorghum are maintained by hand pollinations only

Seed stored at low temperature and low humidity will remain viable for a much longer period than when stored at normal temperatures This is particularly desirable in the tropics where both temperature and humidity may be excessive over a large portion of the year Storage rooms which can be cooled to temperatures of 5 to 10 degrees Centigrade with humidity control will extend the life of the seed for a considerable period of time Control of rodents and insects in stored seed is also important Low temperature storage aids in insect control as well as extending the viability of the seed

Increase and Distribution. Improved varieties will not help the cultivators until they are grown in their fields Organized procedures for increase and distribution of seed of new varieties are necessary if seed is to reach the cultivator rapidly and in large enough quantity to be widely grown In many developing countries, where a strong and efficient private seed industry has not yet developed, this function may be taken over by various government agencies In India the National Seeds Corporation, Ltd , has been formed to serve this function Its organization will be discussed in a later topic In the U S A and many other countries state wide seed certification organizations have developed to assist with increase and distribution of new varieties and to produce pure seed of older varieties

In the increase of seed of new varieties it is important to maintain purity of the seed and produce seed with excellent germination Some principles to follow in increase of new varieties are as follows

1 Seed should be planted on clean ground that did not grow another variety of that crop the preceding year This is necessary to prevent mixture from volunteer plants growing from seed lying over in the soil

2 The field should be free of serious weeds common to the crops so that the crop seed produced will be free of weed seed

3 The variety should have isolation from other varieties of the same crop to prevent mixture resulting from natural cross-pollination The isolation required may be only a few yards for a self pollinated crop like wheat to several hundred yards for a cross pollinated crop

4 The seed should be grown at a high level of fertilization and other good cultural practices followed in order to obtain as large an initial increase of seed as possible

5 Care needs to be taken in threshing, cleaning and bagging the seed to prevent mixture with other varieties or with other crop seeds or weed seeds

6 Treatment of seed with fungicides to control seed borne diseases should be practiced These treatments can be made most efficiently at the time the seed is cleaned and bagged

7 Cool, dry storage needs to be provided in order that germination will not deteriorate before the seed is planted Protection from rodents and insects while the seed is in storage is essential

Initial distribution of seed should be made to experienced seed growers who will follow the practices outlined above Distribution to inexperienced seed growers may result in production of poor quality seed, or low seed yields, or even loss of breeder or foundation seed, thus delaying the final distribution of the new variety to the cultivator

ROLE OF SEED CERTIFICATION

In many countries seed certification organizations have been developed to assist in the production and marketing of pure seed of superior varieties of the major farm and vegetable crops In the U S A. the seed certification organizations have a membership composed of seed growers The seed growers will range from individual cultivators who produce small amounts of a single variety to large seed companies who produce large acreages of many crops The seed certification organization works in close cooperation with the state agricultural departments, who enforce the seed laws of the state, and the state agricultural universities where the new varieties are usually developed Often the seed certification organization will be designated by law as the official certification organization in the state The function of the seed certification organization and its members is to produce, certify, and market pure seed of adapted varieties of the various farm crops Certified seed thus is a source of pure seed which the cultivator can obtain in order to get a start of a new variety, or to renew his seed stocks of an adapted variety if his own seed becomes mixed Certified seed is produced in such a way as to ensure genetic identity and genetic

purity of a particular variety or propagating material

Classes of Certified Seed. Four classes of seed are recognized by seed certification agencies (Fig 19 2)

1 *Breeder seed* Breeder seed is seed or vegetative propagating material directly produced or controlled by the originating plant breeder or institution Breeder seed provides the source for the increase of foundation seed

2 *Foundation seed* Foundation seed is the direct increase from breeder seed The genetic identity and purity of the variety is maintained in foundation seed Production is carefully supervised or approved by representatives of an agricultural experiment station Foundation seed is the source of all certified seed classes, either directly or through registered seed

3 *Registered seed* Registered seed is the progeny of foundation or registered seed Registered seed maintains satisfactory genetic identity and purity of the variety for the production of certified seed Registered seed is used as the source of certified seed

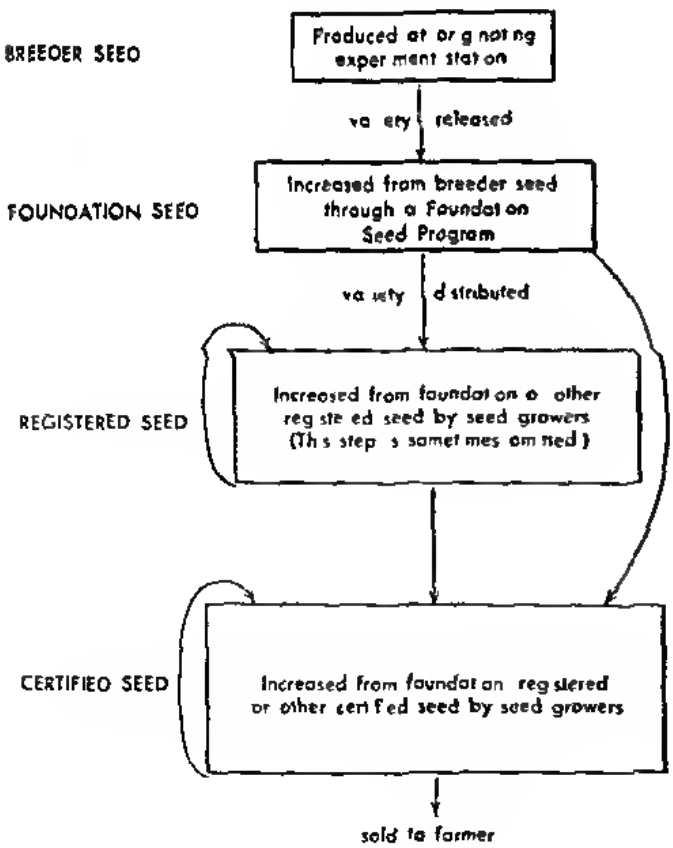

Fig 19 2 Steps in the increase and distribution of a new variety

4 *Certified seed* Certified seed is the progeny of foundation, registered, or certified seed Certified seed must be handled so as to maintain sufficient genetic identity and purity of the variety that it will be approved and certified by the certifying agency

It is not always necessary that all of the above classes of seed be produced For example certified seed may be grown directly from foundation seed thus eliminating the registered class As already stated breeder seed is produced by the originating plant breeder or institution In India foundation seeds of hybrid maize and other crops are produced by the National Seeds Corporation The foundation seeds are made available by them to state seed farms or to private growers for the production of registered or certified seed Procedures for growing foundation seeds are similar to those outlined above for increasing breeder seed

Seed Certification Practices. The production of registered or certified seed by the state seed farm or the private grower requires the utilization of practices similar to those used for the production of breeder seed They may be outlined briefly as follows

1 Plant foundation or registered seed
2 Plant on clean ground free of weeds and other crop plants
3 Plant on land which did not grow previously another variety of the same crop
4 Give sufficient isolation to prevent natural cross-pollination with another variety
5 Avoid mixing in threshing, cleaning and bagging of seed
6 Label the bags correctly as to crop variety, germination, and purity
7 Field inspections and examination of seed for proper labelling to be done by the seed certifying organization

NATIONAL SEEDS CORPORATION

In India, the National Seeds Corporation has been formed to (*a*) promote the development of a seed industry within the country, and (*b*) function as a foundation seed stock organization The National Seeds Corporation was started in 1961 under the auspices of the Indian Council of Agricultural Research and was registered as a corporation in the public sector in 1963

The seed industry had been

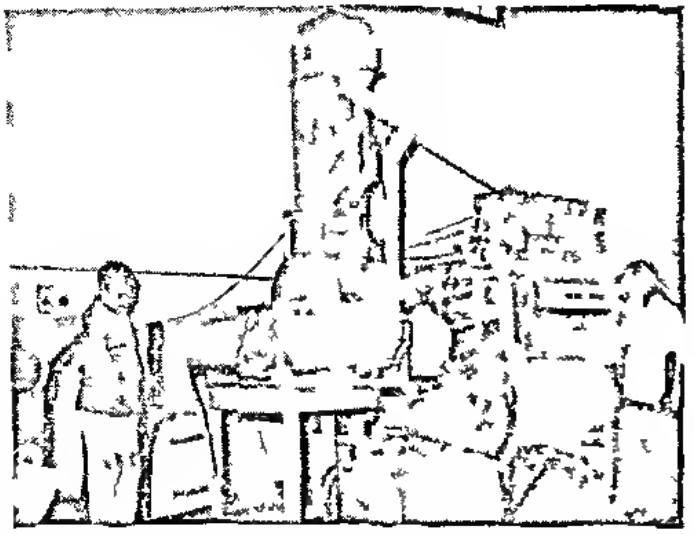

Fig 19 3 Seed is cleaned treated with a fungicide and bagged in official bags of the National Seeds Corporation

in a rather unorganized manner without adequate checks on germination, purity and quality With the development and release of several maize hybrids under the Coordinated Maize Breeding Scheme some organization was required to maintain and produce the inbred lines needed in the production of the maize hybrids and to supervise the production and distribution of single cross and double cross hybrid seed This was the first responsibility given to the National Seeds Corporation Responsibility was later extended to include hybrid sorghum hybrid bajra wheat jute vegetatively propagated forage varieties and various vegetable and other crop seeds Foundation seed is produced on the seed farms of the National Seeds Corporation Certified seed is grown by private growers under the supervision of the National Seeds Corporation Seeds produced by or under the supervision of the National Seeds Corporation are cleaned, treated with proper fungicides, bagged and correctly labelled (Fig 19 3)

SEED LABELLING

Proper and accurate labelling of seed is needed to ensure the cultivator that the seed he obtains is pure and high in quality The label should state (*a*) kind of seed, (*b*) variety, (*c*) germination percentage (*d*) purity, (*e*) weed seed percentage (*f*) inert materials (*g*) date of germination test, (*h*) seller's name and address, (*i*) other information pertinent to the seed or its identification *Accurate labelling* is important to the purchaser (Fig 19 4) To ensure that all seed sold is labelled and that the information supplied on the label is accurate will require some legal means of enforcement This is usually provided in a seed act or through other legislative provisions

SEED TESTING LABORATORIES

Seed testing is done to properly evaluate the germination and purity of seed samples The routine for carrying out a germination test varies with the particular crop seed being tested In any case the seed is maintained at optimum moisture and temperature for the period required for all healthy seeds to germinate Germination tests should be replicated to provide a more accurate estimate of the germination percentage Purity tests are made

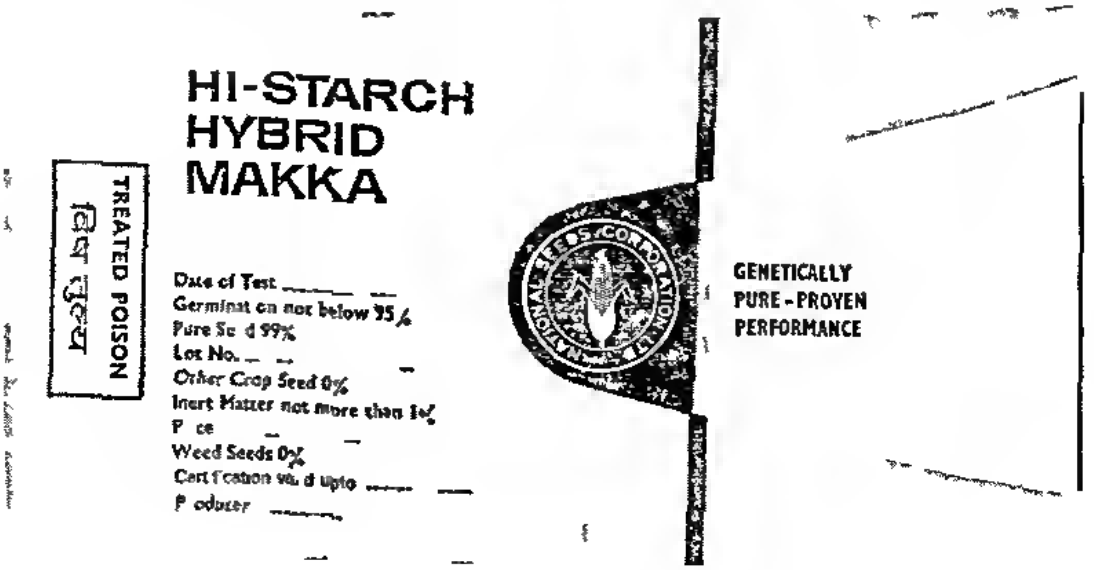

Fig 19 4 Label used by the National Seeds Corporation Ltd for certified seed of the hybrid maize variety 'Hi Starch Hybrid Makka

by physically separating the pure crop seeds from the weed seeds, other crop seeds, and inert material and calculating the percentage of each by weight (Fig 19 5)

Germination standards for good seed vary with different crops Germination in good samples of wheat, rice, maize and many other crops may be quite high, above 90 to 95 percent In other crops such as sorghum it is usually difficult to obtain such high germination In making germination tests of freshly harvested seeds, the problems of seed dormancy must be considered Usually dormancy can be broken by subjecting moist seeds to low temperatures for a few days before starting the germination test

The seed laboratory is an important institution in carrying out a seed production and certification programme The seed laboratory serves the producer of seed by supplying him information on the germination and purity of the seed he produces This is needed for accurate labelling of the seed he sells The seed laboratory serves the seed certification organization in testing seed samples and determining whether they meet the certification requirements The seed laboratory serves the seed law enforcement agency by providing information on the accuracy of labelling of seeds in commerce

Fig 19 5 Examining seeds for purity in a seed testing laboratory The men shown in the seed laboratory are trainees in a seed testing and seed certification training programme conducted by the National Seeds Corporation Ltd , New Delhi, and the U S Agency for International Development

To obtain accurate tests of germination and purity from the seed laboratory it is essential that the seed sample being tested is drawn in such a way that it accurately represents the whole lot of seed If the sample represents a single bag of seed, seed should be taken from two or three places in the bag If the sample represents a large number of bags in a lot of seed, a small sample should be drawn from each bag, or a random selection of bags, and the small samples composited Complete information regarding the identity of the sample should be sent to the seed laboratory

In India seed testing laboratories have been established at the Indian Agricultural Research Institute and in most of the states

AGRICULTURAL INFORMATION AGENCIES

Many good varieties are never grown extensively because (*a*) the cultivator never receives information about the merits of the new variety or (*b*) seed is not made available in quantities to supply the cultivator's needs Education of the cultivator is an important function of the agricultural extension services, agriculture departments, and agricultural colleges and universities, and the community development programmes These organizations can serve effectively by supplying information to the cultivator on the best varieties to grow, by training cultivators and seed growers in the best seed production practices, and by promoting good agricultural practices in general, including utilization of high fertility and pest control so that the improved variety will give maximum performance (Fig 19 6)

PRACTICAL PROBLEMS IN SEED PRODUCTION

Seed production problems are peculiar to each specific crop and in different areas where the crop is grown Solutions to these problems have generally been found by long experience with the crop

Rice, Wheat, Linseed and Pulses. Seed of self-

Fig 19 6 Cultivators being instructed in the best cultural practices for growing a crop of hybrid maize The maximum potential of improved varieties can not be reached with out good cultural practices

pollinated crops such as rice wheat linseed pulses and certain oilseed crops may be replanted again and again without appreciable genetic deteriora tion This is possible because the varieties of self pollinated crops are either pure lines or mixtures of pure lines and do not segregate or cross freely The seed grower or the cultivator may harvest seed from his own crop for successive plantings This practice is satisfactory as long as he can main tain the purity of the variety keep the crop free from other crop and harmful weed seeds control seed borne diseases and produce seed with good germination Normally a small strip around the outside may be harvested for food rather than seed if the crop is planted close to another variety of the same crop Rig d rogu ng to remove off type plants other crop plants or weeds will help to ma ntain the genetic purity of the variety

Open pollinated Maize, Sorghum, Bajra, Cotton and Jute These crops are either largely cross pollinated or partly cross pollinated Mixing as the result of natural cross pollinat on with other varieties in adjacent fields is common Hence seed production fields of these crops will need to be iso lated sufficient distances so that natural cross polli nation does not occur Careful roguing may be used to eliminate off types and maintain uniform ity of type In crops like cotton progeny row selection may be used to maintain foundation seed stocks with further increase subjected to roguing out of off types

Hybrid Maize In normal product on of hybr d maize seed three classes of seed are commonly pro duced namely inbred single cross and double cross Seed of three way crosses top crosses and multiple crosses may be produced under certa n circumstances

Inbred seed requires the most care in product on Small lots of inbreds are maintained by hand polli nations but larger lots may be increased by open pollination in isolated fields (Fig 8 14) Careful roguing is required to remove any off type plants that may have originated from stray pollen Ear to row plantings of inbreds maintained by hand pollinations are used to check trueness to type Cytoplasmic male sterile inbreds are maintained by the same procedures used to produce single crosses The cytoplasmic male sterile line is planted

as the seed parent and the male fertile counterpart as the pollen plant

Single cross seed may be produced in limited amounts by hand pollinations, but larger quantities are usually produced by open pollination of the two inbreds involved in isolation The ratio of ear parent to pollen parent rows generally does not exceed 2 1 Careful roguing must be practiced to remove off type plants or plants of doubtful origin in either parent The roguing may be done any time before harvest in the ear parent, but it must be done before pollen is shed in the pollen parent Rogues should be completely destroyed so that suckers will not develop Generally, a rogue is easily identified among inbred plants since it will show hybrid vigour, unless it is a mechanical mixture of another inbred Plants producing fertile anthers in cytoplasmic male sterile rows should be removed before pollen is shed In the production of cyto plasmic male sterile single cross seed to be used in the production of a double cross, the pollen restor ing potential of the pollen parent should be well known

Double cross seed is produced in large quantities for sale to the cultivator Double cross seed is pro duced in the field in isolation At least 200 to 300 metres should separate the field in which double cross seed is being produced from other fields of maize In the production of maize seed this distance may be modified by planting additional border rows of the pollen parent, the number varies with the distance and the size of the seed field In the production of double cross seed the ratio of ear parent rows to pollen parent rows is usually 3 1 or 4 1 Recognizable rogues are destroyed as in the production of single cross seed Tassels in the seed parent rows are removed before they shed pollen (Fig 8 12) If the seed parent is planted to a cytoplasmic male sterile single cross, plants pro ducing fertile anthers are removed

Hybrid maize seed needs to be dried thoroughly before shelling and bagging Before drying and shelling the ears should be sorted to remove damaged or diseased ears or portions of ears After hybrid maize seed has been dried, it is shelled Grading or sizing of the seed is practiced in countries where mechanical planters are used in order to obtain uniform rates of planting Chemical seed treatments are applied to control seed-borne diseases The seed is then bagged, labelled, and stored Cool, dry storage is required to prevent deterioration in germination and damage to the seed by insects or rodents

Hybrid Sorghum and Hybrid Bajra. The commercial production of hybrid sorghum seed has brought new problems in sorghum seed pro duction Commercial production of hybrid sorghum seed has been made possible by the utilization of cytoplasmic male sterility The classes of seed produced are inbreds and single crosses Both the A line and the B line of the female parent must be maintained as well as the R-line (fertility restoring line) Isolation of the seed field is required in the production of hybrid sorghum seed and the distance required for isolation appears to be greater than for maize As with maize, off type plants or seed parent plants that are shedding pollen, are rogued out Seed is harvested from the female rows only The seed is dried, treated with chemical fungicides, bagged, labelled, and stored in a cool, dry place where it will not be damaged by rodents or insects

Sugarcane. Clones of sugarcane released for cultivation are maintained by the institution respon sible for their release Seedcanes or setts are pro duced by them and supplied to the cultivator In some areas sugar factories may assist with local multiplication and distribution of setts of improved varieties

Tobacco. Tobacco seeds are planted in beds and transplanted to the fields Most varieties of tobacco seed require a short exposure to light to ensure germination The exposure to light must be made when the seed is moist In the area of flue-cured tobacco production of Andhra Pradesh, all tobacco seed is supplied to the growers by the Tobacco Research Institute, Rajahmundry Since a single seed plant of tobacco may produce as many as 2 lakh seeds, the inclusion of a single off-type plant for seed production may result in a large amount of off type plants in the field

Potato. The most difficult problem in the pro duction of seed potato is the production of virus free seed If the viruses of potato, leaf roll, Y, A, X or S, infect the plants in the seed production plot, this will lead to degeneration of the seed potato To aid in the production of virus free seed a potato seed certification system was [illegible] India in 1949 The nucleus seeds were [illegible] hills during April to August wi

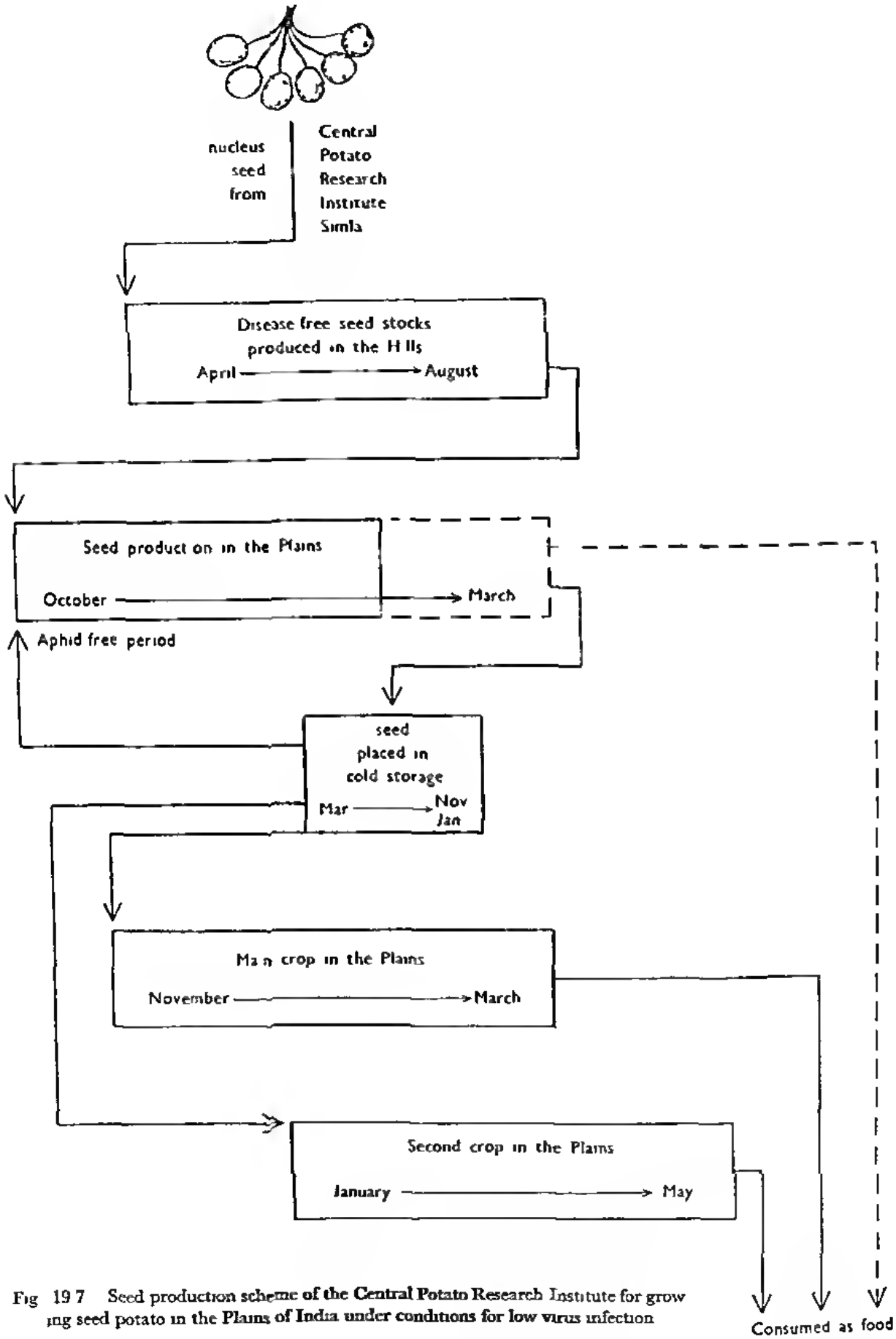

Fig 19 7 Seed production scheme of the Central Potato Research Institute for growing seed potato in the Plains of India under conditions for low virus infection

tion which is the main vector for transmission of the virus is negligible The certified virus free seeds were then transported to the plains for cultivation

This procedure became impracticable as the area planted to potato in the plains increased because (*a*) the suitable land in the hills for potato cultivation was too limited to meet the entire demand for seeds and (*b*) the cost of seeds was high because of transportation charges on the seeds Studies of the aphid population in the plains and hills and other related studies have helped recently to develop a new system of seed production called the Seed plot Technique which aims at production of seeds in the plains area thus relieving the burden on the hill area (Fig 19 7)

The screening of segregating populations from crosses made in the hills and the development of varieties in the plains has already been discussed in Chapter 13 on Breeding Potato In addition nucleus seed may be brought directly from the hills The nucleus seed is grown in the hills in the low aphid period and transported to the plains for cold storage In most places in the plains one crop is grown from November to March while in certain areas two crops of potato are grown the first crop from October to February and the second from end of January to end of April The presence of effective aphid population in the plains spreads from the middle of January to the end of April Thus the potato plants during this period are exposed to infection by the virus The seed production in the plains therefore is done in the first crop season only and the steps in the process are as follows

1 The seed is planted in autumn in the beginning of October

2 The land is not heavily fertilized and the seeds are spaced closely so that large numbers of small seed-sized tubers are formed Unhealthy plants are rogued out

3 Irrigation is restricted towards the middle of December and gradually stopped completely so that the haulms dry up before the aphid population is built up (Fig 19 8) The green haulms may also be killed with weedicides before the middle of January so that the aphids cannot feed on the plants

4 The seeds may be left in the soil and harvested by the end of February or early March If the land is required to be released early the seeds may be harvested earlier and spread thinly in a dark place for thickening of skins

5 The harvested seed is sorted and seeds for the next year are kept in cold storage

About one hectare of seed production plot is necessary to meet the requirement of seeds for 8 to 10 hectares in cultivation The seed for the main

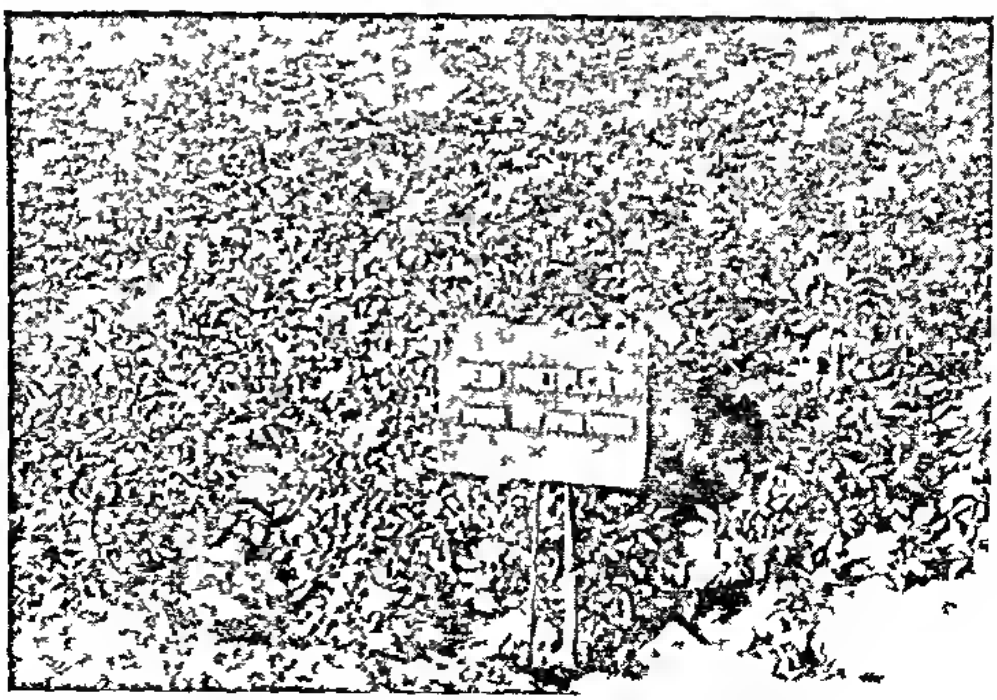

Fig 19 8 Potato seed multiplication field in the Plains near Jullundur Punjab This photo taken about mid December shows a good growth of haulms before the normal increase in the aphid population

crop and the second crop in the plains has to be stored from the autumn crop in the previous season

Forage Crops. The production of forage crop seeds has received very little attention in India and other countries of southeast Asia The seeds of forage crops are multiplied in areas where the climatic conditions favour maximum production of seeds Improved cultural practices like line sowing heavy fertilization, good water management, weeding, and plant protection measures are followed to induce maximum seed set Honey bees may be supplemented to aid cross pollination in certain forage crops like lucerne or berseem

Some forage grasses, such as bermudagrass, which produce little or no seeds, can be propagated vegetatively Such crops are multiplied and distributed through clones In India vegetative cuttings of the Pusa Giant Napier grass is distributed by the National Seeds Corporation

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GLOSSARY

ACCLIMATIZATION the adaptation of an individual to a changed climate, or the adjustment of a species or a population to a changed environment over a number of generations

A LINE the male sterile parent line in a cross being made to produce hybrid seed Commonly used with reference to hybrid sorghum, hybrid wheat, etc

ALLELE an alternative gene Alleles are located on corresponding loci of homologous chromosomes Also ALLEL, ALLELOMORPH

ALLOPLOM OR ALLOPOLYPLOID an organism with more than two sets of chromosomes in its body cells, each set derived from a different species

AMPHIPLOM or AMPHIDIPLOID an individual originating by hybridization between species and possessing the total chromosome complement of the parent species Generally produced by doubling the chromosome number of the F_1 hybrid plant

ANEUPLOM an individual with other than an exact multiple of the haploid chromosome complement.

ANTHER the pollen bearing portion of the stamen

ANTHESIS the process of dehiscence of the anthers, the period of pollen distribution

APETALOUS FLOWER flower without petals

APOMIXIS reproduction from an unfertilized egg or from somatic cells associated with the egg

AREA CROSS groups of self sterile arrows of sugarcane brought together in isolation for pollination by a common male

ASEXUAL REPRODUCTION reproductive process which does not involve the union of gametes

AUTOPLOM or AUTOPOLYPLOID an organism with more than two sets of chromosomes in its body cells, both sets derived from the same species

BACKCROSS (1) in breeding, a cross of a hybrid with one of its parents or with a genetically equivalent organism, (2) in genetics, a cross of a hybrid with a homozygous recessive (See also TESTCROSS)

BC_1, BC_2, etc symbols used to designate the first backcross generation, the second backcross generation etc

BIOMETRY the science dealing with the application of statistical methods to biological problems

BIOTYPE a population in which all individuals have an identical genotype

B LINE the fertile counterpart of the A line The B-line does not have fertility restoring genes and is used as the male parent to maintain the A line

BREEDER SEED seed (or vegetative propagating material) increased by the originating, or sponsoring, plant breeder or institution and which is used as the source for the increase of foundation seed

CERTIFIED SEED the progeny of foundation, registered, or certified seed, produced and handled so as to maintain satisfactory genetic identity and purity, and approved and certified by an official certifying agency

CHARACTER the expression of a gene as revealed in the phenotype

CHROMATID one of two threadlike structures formed in the duplication of a chromosome to form daughter chromosomes

CHROMOSOME a structural unit in the nucleus which carries the genes in a linear constant order, it preserves its individuality from one cell generation to the next and is typically constant in number in any species

CLEISTOGAMY pollination and fertilization in an unopened flower bud

CLONE a group of plants originating by vegetative propagation from a single plant

COMBINING ABILITY, GENERAL the average or over all performance of a genetic strain in a series of crosses

COMBINING ABILITY, SPECIFIC the performance of specific combinations of genetic strains in crosses in relation to the average performance of all combinations

COMPLETE FLOWERS flowers having all usual parts (sepals, petals, stamens, and pistils)

COROLLA the petals considered collectively

CORRELATION a mutual relationship between two things such that an increase or decrease of one is generally associated with an increase or decrease of the other Linear correlation is measured by the CORRELATION COEFFICIENT which may range in value from -1 to $+1$

CROSS FERTILIZATION see FERTILIZATION

CROSS POLLINATION see POLLINATION

CROSSING OVER an interchange of segments between the chromatids of two homologous chromosomes at meiosis

CROSSOVER VALUE the percentage of crossing over in a hybrid population a term used mostly in determining linkage percentage particularly in chromosome mapping

CULTIVAR a variety

CYTOLOGY the science dealing with the structure, function and life history of the cell

CYTOPLASM the protoplasm of a cell excluding the nucleus

CYTOPLASMIC pertaining to or centred in the cytoplasm

CYTOPLASMIC INHERITANCE inheritance dependent upon hereditary units in the cytoplasm

DEHISCENCE splitting open of a fruiting structure or anther

DESI Local or native

DETASSEL removal of the immature tassel as practiced in the production of hybrid seed corn

DETERMINATE descriptive of an inflorescence in which the terminal flower opens first, thus arresting the prolongation of the floral axis Example, a cyme

DIHYBRID the result of a cross between parents which differ by two specified genes

DIOECIOUS having staminate and pistillate flowers on different plants of the same species

DIPLOID having two sets (genomes) of chromosomes, chromosome number of $2n$, as in a zygote Somatic or body tissue is normally diploid in contrast to haploid germ cells

DOMINANT (1) a gene that expresses itself in a hybrid to the exclusion of its contrasting (recessive) allele, (2) a character which is expressed in a hybrid phenotype to the exclusion of the contrasting (recessive) character

DUPLICATE GENES two or more pairs of genes that produce identical effects, whether alone or together

EGG the female gamete or germ cell

EMASCULATE to remove the anthers from a bud or flower before pollen is shed Emasculation is a normal preliminary step in crossing to prevent self pollination

EMBRYO the rudimentary plant in a seed The embryo arises from the zygote

EMBRYO SAC typically, an eight nucleate female gametophyte The embryo sac arises from the megaspore by successive mitotic divisions

ENDOSPERM triploid tissue which arises from the triple fusion of a sperm nuclei with the polar nuclei of the embryo sac In seeds of certain species, the endosperm persists as a storage tissue and is used in the growth of the embryo and by the seedling during germination

EPIPHYTOTIC sudden and usually widespred development of a destructive disease in plants

EPISTASIS interaction between nonallelic genes in which a gene or combination of genes exerts a dominant effect over another gene or combination of genes

F_1, F_2, etc symbols used to designate the first generation, the second generation, etc , after a cross

FATUOID a mutant commonly occurring in cultivated oats and which resembles wild oats (*Avena fatua*)

FERTILIZATION union of an egg and a sperm (gametes) to form a zygote SELF FERTILIZATION is the union of an egg with a sperm from the same flower or from another flower on the same plant, or within a clone CROSS FERTILIZATION is the union of an egg with a sperm from a plant of a different clone

FILAMENT the stalk of the stamen which supports the anther

FLORET a small flower from an inflorescence, as in a grass panicle or a composite head

FOUNDATION SEED seed stocks increased from breeder seed, and so handled as to closely maintain the genetic identity and purity of a variety Production of foundation seed is carefully supervised or approved by representatives of an agricultural experiment station Foundation seed is the source of certi

fied seed, either directly or through registered seed

FUZZ the seeds and attached floral structures of sugarcane Also called FLUFF

GENE the unit of inheritance, located on the chromosome, by interaction with other genes, the cytoplasm, and the environment, it affects or controls the development of a character

GENE INTERACTION modification of gene action by a nonallelic gene

GENETICS the science dealing with heredity

GENOME a set of chromosomes, such as contained within a gamete, corresponds to the haploid number of chromosomes within the species

GENOTYPE (1) the genetic makeup of an organism—the sum total of its genes, both dominant and recessive, (2) a group of organisms with the same genetic make up

GENOTYPIC RATIO the proportions of the different genotypes in a particular progeny

GERM PLASM (1) the material basis of heredity, (2) the potential hereditary materials within a species taken collectively

GLUME the outer husks or bracts of each spikelet in grasses

HAPLOID having a single set (genome) of chromosomes in a cell or an individual, the reduced number (n), as in a gamete

HEAVING lifting effect of the soil due to alternate freezing and thawing Heaving may result in the lifting up of plants, and may tear them loose from the soil, or shear off roots

HEREDITY the transmission of genetic characters from parents to progeny, the genetic characters transmitted to an individual by its parents

HERITABILITY capability of being inherited, that portion of the observed variance in a progeny that is inherited

HETEROSIS (HYBRID VIGOUR) (1) the increased vigour, growth, size, yield or function of a hybrid progeny over the parents that results from crossing genetically unlike organisms, (2) the increase in vigour or growth of a hybrid progeny in relation to the average of the parents

HETEROZYGOTE an organism with one or more heterozygous pairs of genes An organism that will not breed true

HETEROZYGOUS having unlike alleles at corresponding loci of homologous chromosomes An organism may be heterozygous for one, or several genes (see also HOMOZYGOUS)

HEXAPLOID having six sets (genomes) of chromosomes, chromosome number of $6n$

HOMOLOG a homologous chromosome

HOMOLOGOUS CHROMOSOMES chromosomes which synapse or pair at the first division in meiosis Each member of a pair has a corresponding sequence of gene loci and is derived from a different parent

HOMOZYGOUS having like genes at corresponding loci on homologous chromosomes An organism may be homozygous for one, several, or all genes (See also HETEROZYGOUS)

HYBRID (1) the first generation offspring of a cross between two individuals differing in one or more genes (2) the progeny of a cross between species of the same genus or of different genera

HYBRIDIZATION (1) the crossing of individuals of unlike genetic constitution, (2) a method of breeding new varieties which utilizes crossing to obtain genetic recombinations

HYBRIDIZE to produce hybrids by crossing individuals with different genotypes

HYBRID VIGOUR see HETEROSIS

I_1 I_2 etc symbols used to designate the first inbred generation second inbred generation, etc (See also S_1 S_2 etc)

IMMUNE free from attack by a given pathogen, not subject to the disease

IMPERFECT FLOWER a flower lacking either stamens or pistils (See also PERFECT FLOWER)

INBRED LINE (1) a pure line usually originating by self pollination and selection, (2) the product of inbreeding

INBREEDING breeding closely related organisms, in plants, usually by self pollination

INCOMPATIBILITY failure to obtain fertilization and seed formation after self pollination, usually due to slow pollen tube growth in the stylar tissue

INCOMPLETE DOMINANCE the production of an effect by two different alleles that is intermediate to the effects produced by the same alleles in a homozygous condition

INCOMPLETE FLOWER a flower lacking one or more of the four essential flower parts (See also COMPLETE FLOWER.)

INDEPENDENT ASSORTMENT the chance distribution of two or more pairs of segregating genes to the gametes

INDETERMINATE descriptive of an inflorescence in which the terminal flower is last to open The flowers arise from axillary buds, and the floral axis may be indefinitely prolonged by a terminal bud Example, a raceme

INFLORESCENCE (1) a flower cluster, (2) the arrangement and mode of development of the flowers on a floral axis

INHERIT receiving from one's predecessors In organisms, chromosomes and genes are transmitted from one generation to the next

INOCULATE (1) to place inoculum where it will produce an infectious disease, (2) to introduce nitrogen fixing bacteria into the soil, usually by treating seeds before sowing

INOCULUM spores, bacteria or fragments of mycelium of pathogens which can infect plants, or soil

IRRADIATION in genetics and plant breeding, exposing seed pollen, or other plant parts to x rays or other radiations to increase mutation rates

IRRADIATION BREEDING the use of irradiation to increase mutation rates for the purpose of obtaining mutant plants that may be useful in the development of improved varieties

KHARIF the summer season

LEMMA the lower of the two bracts enclosing each floret in the grass spikelet

LINE a group of individuals from a common ancestry A more narrowly defined group than a strain or variety

LINKAGE the relationship between two or more genes that tend to be inherited together because they are located in the same chromosome This results in parental combinations occurring more frequently than recombinations in the progeny

LINKAGE GROUP a group of genes arranged in a linear order on a chromosome

LINKAGE MAP a diagram of a chromosome showing the relative position of the genes

LOCUS the position of a particular gene on a chromosome (plural, Loci)

LODICULE one of two scalelike structures at the base of the ovary in a grass flower

M_1, M_2, etc symbols used to designate the first generation, second generation, etc following exposure to mutagenic agents (ionizing radiations, chemical mutagens, etc) (Also, see R_1, R_2, etc.)

MALE STERILITY a condition in which pollen is absent or nonfunctional in flowering plants

MASS SELECTION a system of breeding in which seed from individuals selected on the basis of phenotype is composited and used to grow the next generation

MEGAGAMETOPHYTE see EMBRYO SAC

MEGASPORE one of the four haploid spores originating from the meiotic divisions of the diploid megaspore mother cell in the ovary and which gives rise to the megagametophyte

MEGASPORE MOTHER CELL diploid cell in ovary which gives rise, through meiosis, to four haploid megaspores

MEIOSIS two successive nuclear divisions, in the course of which the diploid chromosome number is reduced to the haploid

MELTING POT groups of arrows of sugarcane brought together in isolation to permit natural cross pollination A polycross

MICROSPORE one of the four haploid spores originating from the meiotic division of the microspore mother cell in the anther which gives rise to the pollen grain

MICROSPORE MOTHER CELL diploid cell in the anther which gives rise, through meiosis, to four haploid microspores

MITOSIS a process of nuclear division in which the chromosomes are duplicated longitudinally, forming two daughter nuclei each having a chromosome complement equal to that of the original nucleus

MONOECIOUS having staminate and pistillate flowers on the same plant

MONOHYBRID the result of a cross between parents which differ by one specified gene

MONOSOME a chromosome which has no homolog present A haploid chromosome in an otherwise normal diploid individual

MONOSOMIC a plant with a chromosome which has no homolog present (monosome)

MULTIPLE ALLELES a series of alleles, or alternative forms, of a gene A normal heterozygous diploid plant would bear only two genes of an allelic series Multiple alleles arise by repeated mutations of a gene, each mutant giving different effects

MULTIPLE GENES two or more independent pairs of genes which produce complementary or cumulative effects upon a single character of the phenotype

MUTANT an organism which has acquired a heritable variation as a result of mutation

MUTATION a sudden variation in the hereditary material of a cell Mutations may be gene mutations or chromosomal changes A gene mutation is a change in a gene from one allelic form to another Chromosomal changes include deletions, duplications, inversions interchanges, etc

NOBLIZATION a term used in sugarcane breeding to denote the crossing of *Saccharum officinarum* with related species, followed by one or more backcrosses to *S officinarum*

NONRECURRENT PARENT parent which is not involved in a backcross (See also RECURRENT PARENT)

NULLISOMIC an otherwise normal diploid plant that lacks a specific chromosome pair

OUTCROSS cross pollination, usually by natural means, with a plant different in genetic constitution

OVARY the enlarged basal portion of the pistil, in which the seeds are borne

OVULE the structure which bears the female gamete and becomes the seed after fertilization

PALEA the upper of the two bracts enclosing each floret in the grass spikelet

PANICLE an open and branched inflorescence with pediceled flowers

PARTHENOCARPY the production of fruits without fertilization and, normally, without seeds

PARTHENOGENESIS the development of an individual from a gamete without fertilization

PARTIAL DOMINANCE lack of complete dominance, the production of a hybrid intermediate between the parental types (See also INCOMPLETE DOMINANCE)

PATHOGEN an organism capable of inciting a disease

PATHOGENICITY the ability of an organism to incite a disease

PENTAPLOID having five sets (genomes) of chromosomes, chromosome number of $5n$

PERFECT FLOWER flower possessing both stamens and pistils (See also IMPERFECT FLOWER)

PHENOTYPE (1) physical or external appearance of an organism as contrasted with its genetic constitution (genotype), (2) a group of organisms with similar physical or external makeup

PHENOTYPIC RATIO the proportions of the different phenotypes in a particular progeny

PHYSIOLOGIC RACE pathogens of the same species and variety, which are structurally similar but which differ in physiological and pathological characteristics, especially in ability to parasitize varieties of a particular host

PISTIL the seed bearing organ in the flower, composed of the ovary, the style, and the stigma

PISTILLATE FLOWER a flower bearing pistils but no stamens

PLASMAGENE a cytoplasmic borne unit of heredity

POLAR NUCLEI two centrally located nuclei in the embryo sac which unite with the second sperm in a triple fusion In certain seeds the product of this triple fusion develops into the endosperm

POLLEN GRAIN the male gametophyte, originating from a microspore

POLLEN MOTHER CELL see MICROSPORE MOTHER CELL

POLLEN TUBE a tube developing from the germinating pollen grain The sperm cells pass through the pollen tube to reach the ovule

POLLINATION transfer of pollen from the anther to a stigma SELF POLLINATION is the transfer of pollen from an anther to the stigma of the same flower or another flower on the same plant, or within a clone

CROSS POLLINATION is the transfer of pollen from an anther on one plant to a stigma in a flower on a different plant.

POLYCROSS an isolated group of plants or clones arranged in some fashion to facilitate random interpollination

POLYCROSS PROGENY progeny from a selection, line, or clone outcrossed to other selections growing in the same isolated polycross nursery

POLYPLOID an organism with more than two sets (genomes) of chromosomes in its body cells

PROGENY SELECTION selection based on progeny performance

PROGENY TEST a progeny, or groups of progenies, grown for the purpose of evaluating the genotype of the parent

PURE LINE a strain in which all members have descended by self fertilization from a single homozygous individual A pure line is [illegible] (homozygous)

QUANTITATIVE [illegible]

influenced by a series of independent genes which are cumulative in their effect

R_1, R_2, etc *symbols* used to designate the first generation, second generation, etc following exposure of seeds or plants to ionizing radiations (Also, see M_1 M_2, etc)

RABI the winter season

RECESSIVE the condition of a gene such that it does not express itself in the presence of the contrasting (dominant) allele

RECIPROCAL CROSSES two crosses between two plants or strains in which the male parent of one cross is the female parent of the second cross, for example, $A \times B$ and $B \times A$

RECIPROCAL RECURRENT SELECTION a recurrent selection breeding system in which genetically different groups are maintained and in each selection cycle individuals are mated from the different groups to test for combining ability

RECOMBINATION formation of new gene combinations as a result of cross fertilization between individuals differing in genotype

RECURRENT PARENT parent to which hybrid material is crossed in a backcross (See also NONRECURRENT PARENT)

RECURRENT SELECTION a breeding system designed to increase the frequency of favourable genes for yield or other characteristics by repeated cycles of selection

REDUCTION DIVISION a nuclear division in which the chromosomes are reduced from the diploid to the haploid number (See also MEIOSIS)

REGISTERED SEED the progeny of foundation or registered seed produced and handled so as to maintain satisfactory genetic identity and purity, and approved and certified by an official certifying agency Registered seed is normally grown for the production of certified seed

RESISTANT characteristic of a host plant such that it is capable of suppressing or retarding the development of a pathogen or other injurious factor

RHIZOME an underground stem, usually horizontal and often elongated, distinguished from a root by the presence of nodes and internodes and sometimes scalelike leaves and buds at the nodes

S_0 *symbol used to designate the original selfed* plant

S_1, S_2, etc symbols for designating first selfed generation (progeny of S_0 plant), second selfed generation (progeny of S_1 plant), etc

SEED a mature ovule *with its normal coverings* A seed consists of the seed coat embryo, and, in certain plants, an endosperm

SEGREGATION the separation of homologous chromosomes (and genes) from different parents at meiosis

SELECTION (1) any process, natural or artificial, which permits an increase in the proportion of certain genotypes or groups of genotypes in succeeding generations, (2) a plant, line, or strain which originated by a selection process

SELF FERTILE capable of fertilization and setting seed after self pollination

SELF-STERILITY failure to complete fertilization and obtain seed after self pollination

SETT a stem cutting used for asexual propagation of sugarcane Also called seedcanes

SEXUAL REPRODUCTION reproduction involving germ cells and union of gametes

SOMATIC referring to diploid body cells, normally with one set of chromosomes coming from the male parent and one set from the female parent

SPECIES a unit in classification, a subdivision of a genus A group of closely related individuals descendent from the same stock

SPERM a male gamete

SPIKE an inflorescence with a more or less elongated axis, along which the flowers are sessile or nearly so

SPIKELET a unit of the inflorescence in the grasses, composed of the glumes, the rachilla, and the florets

SQUARE an unopened flowerbud in cotton with its accompanying bracts

STAMEN the pollen bearing organ in the flower, composed of an anther and a filament

STAMINATE FLOWER a flower bearing stamens but no pistil

STERILITY failure to complete fertilization and obtain seed as a result of defective pollen or ovules, or other aberrations

STIGMA the portion of the pistil which receives the pollen

STOLON a trailing stem, capable of forming roots and shoots from its nodes

STRAIN a group of individuals *from* a common origin Generally, a more narrowly defined group than a variety.

STYLE the stalk connecting the ovary and the stigma.

SUSCEPTIBLE characteristic of a host plant such that it is incapable of suppressing or retarding an injurious pathogen or other factor

SYNTHETIC VARIETY advanced generations of open pollinated seed mixtures of a group of strains, clones, or inbreds, or of hybrids among them

TESTCROSS a cross of a hybrid with one of its parents, or to a genetically equivalent homozygous recessive Used to test for homozygosity or for linkage

TETRAPLOID having four sets (genomes) of chromosomes, chromosome number of $4n$

TOP CROSS an outcross of selections clones, lines, or inbreds, to a common pollen parent In maize, commonly an inbred variety cross

TOP CROSS PROGENY progeny from outcrossed seed of selections, clones, or lines to a common pollen parent

TRANSGRESSIVE SEGREGATION the segregation of individuals, in the F_2 or a later generation of a cross, which show a more extreme development of a character than either parent

TRIHYBRID resulting from a cross between parents which differ by three specified genes

TRIPLOID having three sets (genomes) of chromosomes, chromosome number of $3n$

VARIANCE the average of the squared deviations about a mean.

VARIANCE, ENVIRONMENTAL the variance resulting from environmental or nongenetic causes

VARIANCE, GENETIC the variance resulting from genetic causes

VARIANCE, PHENOTYPIC the total variance, the sum of the environmental and the genetic variance

VARIETY a subdivision of a species An agricultural variety is a group of similar plants which by structural features and performance can be identified from other varieties within the same species

VERNALIZATION the treatment of seeds before sowing to hasten flowering Vernalization may be accomplished in certain species by exposure of germinating seeds to temperatures slightly above freezing

VIRULENCE relative capacity of a pathogen to incite a disease

WORLD COLLECTION a collection of germ plasm of a particular species from different geographic locations, used as source materials in plant breeding

XENIA the immediate effect of pollen on the character of the endosperm

ZYGOTE the cell resulting from the fusion of the gametes

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