CHAPTER 22

HYBRID VARIETIES

22.1. INTRODUCTION

The two important features of cross-pollinated species are inbreeding depression and heterosis. Population improvement schemes generally aim at keeping inbreeding at a low level to avoid its ill effects, but an effort to exploit heterosis is rarely made. Heterosis is the basis for the breeding of hybrid and synthetic varieties. In fact, hybrid varieties are the best means of utilizing heterosis. Synthetic varieties utilize only a part of heterosis, but under certain situations they offer the only practical means for it. Hybrid and synthetic varieties have been highly successful in many cross-pollinated species, *e.g.*, maize, jowar and bajra, and even in some self-pollinated species, *e.g.*, cotton, rice and tomato. In India, almost all the recommended varieties of maize today are either hybrid or composite varieties. As in the other chapters on cross-pollinated crop species, more is known about hybrid and synthetic varieties in maize than in all the other crops combined. Our discussion would naturally be primarily based on the knowledge gained from maize, but it is equally applicable to other crop species.

22.2. DEFINITIONS

Hybrid varieties are the first generations (F_1) ***from crosses between two purelines, inbreds,***

open-pollinated varieties, clones or other populations that are genetically dissimilar. Most of the commercial hybrid varieties are F_1's from two or more purelines (rice, tomato) or inbreds (maize, jowar, *S. bicolor*, bajra, *P. glaucum*). An ***inbred*** is a nearly homozygous line obtained through continuous inbreeding of a cross-pollinated species with selection accompanying inbreeding; it is maintained by close inbreeding, preferably by self-pollination. When two inbreds, say A and B, are crossed, the hybrid (A × B) is known as ***single cross***. When two single crosses, say, (A × B) and (C × D), are crossed, the resulting hybrid population, (A × B) × (C × D), is known as ***double cross***. Thus a double cross involves four inbreds, which are first mated to produce two single crosses; the single crosses are then hybridized to yield the double cross. A ***three-way cross*** is a cross between a single cross (A × B) and an inbred (C) to yield the hybrid population (A × B) × C. In addition, there are several other types of hybrids, the more important of which are summarised in Table 22.1.

TABLE 22.1

Types of hybrids. The ultimate aim, however, is to produce single cross hybrids. (Based on Dhillon, 1998; in Banga and Banga, 1998)

Hybrid	*Notation/description**	*Remarks*
Single cross	$I_1 \times I_2$	Common commercially; breeding simpler and faster; greatest exploitation of heterosis; theoretical order of superiority: single cross > three-way cross > double cross; only single cross hybrids are homogeneous, while all others are heterogeneous; single cross hybrids with stable performance can be identified; seed production of single crosses is more rapid and less cumbersome than that of others; genetic variation and expected response to selection among single crosses is the highest, followed by three-way and double crosses
Double cross	$(I_1 \times I_2) \times (I_3 \times I_4)$	
Three-way cross	$(I_1 \times I_2) \times I_3$	
Modified single cross	$(I_1 \times I_1') \times I_2$	
Double modified single cross	$(I_1 \times I_1') \times (I_2 \times I_2')$	
Modified three-way cross	$(I_1 \times I_2) \times I_3'$	
Varietal hybrid	$V_1 \times V_2$	These are more variable, expected to be more stable, seed production is easier, maintenance of genetic purity is difficult and they lack phenotypic appeal. Double topcross hybrids are in cultivation in India and Pakistan
Topcross hybrid	$V_1 \times I_1$	
Double topcross hybrid	$(I_1 \times I_2) \times V_1$	

*1. I_1, I_2, etc. are inbreds.

2. I_1', I_2', etc. are sister inbreds of I_1, I_2, etc., respectively. Two inbreds are called ***sister inbreds*** if their genetic commonality is 50% are more.

3. V_1, V_2, etc. are varieties (open-pollinated).

When an inbred is crossed with an open-pollinated variety, it is known as ***inbred-variety cross*** or ***topcross***. Topcross, however, also denotes crosses of selected plants, lines or clones with an open-pollinated variety. *The purpose of topcross is to estimate GCA of the plants or lines crossed with the open-pollinated variety.* When cross is made to assess combining ability, it is known as ***testcross;*** a testcross may be made with an inbred (for SCA), hybrid, synthetic or open-pollinated variety (for GCA). The common parent used in the testcross is known as ***tester***, and the progeny derived from these crosses are known as ***testcross progeny.*** Another term that deserves mention is polycross. ***Polycross*** denotes the progeny of a line produced through random pollination by a number of selected lines. We shall return to polycross in connection with synthetic varieties. When two open-pollinated varieties are mated, it is usually known as ***varietal*** or ***population cross.***

22.3. HYBRID VARIETIES

When F_1 generation from a cross between two or more purelines, inbreds, clones or other genetically dissimilar populations/lines is used for commercial cultivation, it is called ***hybrid variety***. Hybrid varieties are the most potent means for the exploitation of heterosis. The concept and the methods for hybrid cultivar development originated with maize when it was realized that selection schemes were unable to improve yield.

22.3.1. History

Hybrid varieties were first commercially exploited in maize. The use of hybrid varieties was, ironically, not prompted by the superiority of bybrids, but by the realization that mass and progeny selections were not able to improve the yielding ability of open-pollinated varieties to any substantial extent. As early as 1878, Beal had shown that certain varietal crosses showed substantial (up to 52%) heterosis; he suggested that such varietal hybrids may be used as varieties. Varietal hybrids were indeed grown commercially on a small scale. In 1909, Shull suggested that inbreds should be developed from open-pollinated varieties by continued self-fertilization. The inbreds that combined well to produce superior hybrids should then be crossed to produce single cross hybrid varieties. Shull's scheme could be not be exploited commercially because of the following reasons.

1. Outstanding inbreds that would produce hybrids with yielding abilities substantially higher than those of open-pollinated varieties were not available.
2. Since the female parent was an inbred, the amount of hybrid seed produced per acre was low (30-40 per cent of the open-pollinated varieties). *Consequently, the hybrid seed was expensive.*
3. The male parent was also an inbred; hence pollen production was poor. Consequently, more area had to be planted under the male parent. *This made the hybrid seed more expensive.*
4. The hybrid seed was often poorly developed as it was produced by an inbred and had a relatively poor germination making a higher seed rate necessary.

In 1912, East and Hayes advocated the adoption of heterosis breeding as an alternative breeding strategy. The last three of the difficulties in the Shull's scheme were overcome by the double cross scheme proposed by Jones in 1918. Since in a double cross the female as well as the male parents are single crosses, seed and pollen production are abundant, seed quality and germination are high and, as a result, the cost of the hybrid seed is low. The idea of double cross was adopted soon after it was proposed; the first commercial variety (Burr Leaming Dent) was released in 1922. Popularisation of commercial hybrid varieties in U.S.A. was slow; in 1933, only 0.4% of the maize area was occupied by hybrids. But subsequently, double cross hybrids became popular rapidly so that by 1944 about 80 per cent of the area under maize was under hybrid varieties; by the late 1950s and early 1960s, the open-pollinated varieties were completely replaced by hybrid varieties. It is believed that in U.S.A. hybrid varieties represented, on an average, an yield increase of about 20 per cent over the open-pollinated varieties. In India, this increase has been estimated to be still higher, *viz.*, 30-50 per cent.

The concept of topcross hybrids for preliminary screening of inbreds was proposed by Davis in 1927. In 1934, Jenkins provided a reliable method for the prediction of double cross performance. One year later, in 1935, he proposed the scheme for early testing of inbred lines during inbred development. The utilization of cytoplasmic-genetic male sterility is one of the significant landmarks in the development of hybrid varieties. The Texas cytoplasmic male sterility was identified in 1938, and it was commercially exploited for hybrid seed production during the late 1960s. Subsequently, population improvement of the source populations and the improvement of inbreds markedly increased the yielding ability of inbreds. As a result, by 1960 single crosses had become widely accepted in U.S.A. at the expense of double crosses. Today in U.S.A., single cross maize hybrids have virtually replaced double cross varieties.

In India, intensive research for the development of hybrid maize began in 1952 when the Coordinated Maize Improvement Project began in collaboration with the Rockefeller Foundation. A large number of inbreds and other germplasm were introduced from U.S.A.; the inbreds were used for the production of hybrid maize. Attempts to isolate superior inbreds from the indigenous germplasm have not been much successful. Four hybrids were released in 1961; these were Ganga 1, Ganga 101, Ranjit and Deccan (Table 22.2). Subsequently, in 1961, work on hybrid varieties in jowar and bajra was taken up; these were based on the cytoplamic-genetic male sterility of Combine Kafir 60 and Tift23A, respectively. The first hybrid variety of jowar, CSH1, was released in 1964, while that of bajra, HB1 (HB = hybrid bajra), was released a little later in the same year. However, some bajra hybrids developed without the use of male sterility were released much earlier than this, *e.g.*, Hybrid X_1 and Hybrid X_2 in 1949 (Bombay State, 25 per cent higher yield over the best varieties), and Hybrid 28-15-1 × AF-3-9-1 in 1955 (Maharashtra, 10 per cent more yield).

Hybrid maize could not become very popular in India for several reasons, including (1) the intensive management and input requirements for hybrids, and (2) the need for changing the seed every year. Subsequently, development of composite varieties was undertaken; in 1967 six composite varieties, *e.g.*, Vijay, Kisan, Amber, etc., were released. Today the emphasis of the Coordinated Maize Improvement Project is on the development of composite varieties and on population improvement. But in jowar and bajra, hybrid varieties remain the breeding objective.

22.3.2. Operations in the Production of Hybrid Varieties

In the production of commercial hybrid varieties of sexually propagated species, inbreds are highly desirable in comparison to open-pollinated varieties or other populations with a broad genetic base. This is because (1) inbreds can be maintained indefinitely without a change in their genotype, while the genetic make-up of open-pollinated varieties is likely to be modified by the evolutionary forces (Chapter 11); (2) the hybrids derived from inbreds are

TABLE 22.2

A list of the first released hybrid varieties of different crops in India

Crop	*Year*	*Hybrid variety*	*Type of hybrid*	*Seed production based on*
Maize*	1961	Ganga 101, Ganga 1, Deccan, Ranjit	Double cross	CMS
	1993	Trishulata, DHM107, DHM109	Three-way cross	CMS
	—	JH1121	Single cross	CMS
Sorghum	1964	CSH1	Single cross	CMS
Pearlmillet (bajra)	1965	HB1	Single cross	CMS
Castor	1968	GCH3	Single cross	Pistiilateness
Cotton	1970	H4	Single cross, intraspecific	Manual
	1974	CBS156	Single cross, interspefic	Manual
	1985	DH-7	Single cross, *desi* cotton hybrid	Manual
Tomato	1973	—	Single cross	Manual
Sunflower	1980	BSH1	Single cross	CMS
Pigeonpea	1991	ICPH-8	Single cross	Genetic male sterility
Rapeseed (gobhisarson)	1994	PGSH51	Single cross	CMS
Rice	1996	—	Single cross	CMS
Tobacco	1996	GTH1	—	—
Rice (Basmati)	2001	PRH10 (Pusa Rice Hybrid 10)	Single cross	CMS
Safflower	—	DSH-129	—	—

*Burr Leaming Dent was the first maize hybrid released in USA in 1922.

homogeneous, or nearly so, year after year, while those produced from open-pollinated varieties are likely to be variable, and hence their performance cannot be accurately predicted; and (3) the uniformity of inbred-derived hybrids is also desirable from the viewpoint of uniform quality of the produce. For these reasons, hybrid varieties in case of maize and other crops are produced almost exclusively from inbred lines. The operations involved in the production of hybrid varieties in such a case are as follows: (1) development of inbred lines, (2) evaluation of inbreds, and (3) production of hybrid seed (Fig. 22.1).

22.4. DEVELOPMENT OF INBREDS

Inbred lines are developed from a genetically variable population through continued inbreeding. The population from which inbreds are isolated is known as the ***source population***. The source population is generally an open-pollinated variety, but it may as well be a synthetic, a single cross or a double cross. Inbreds isolated from an open-pollinated

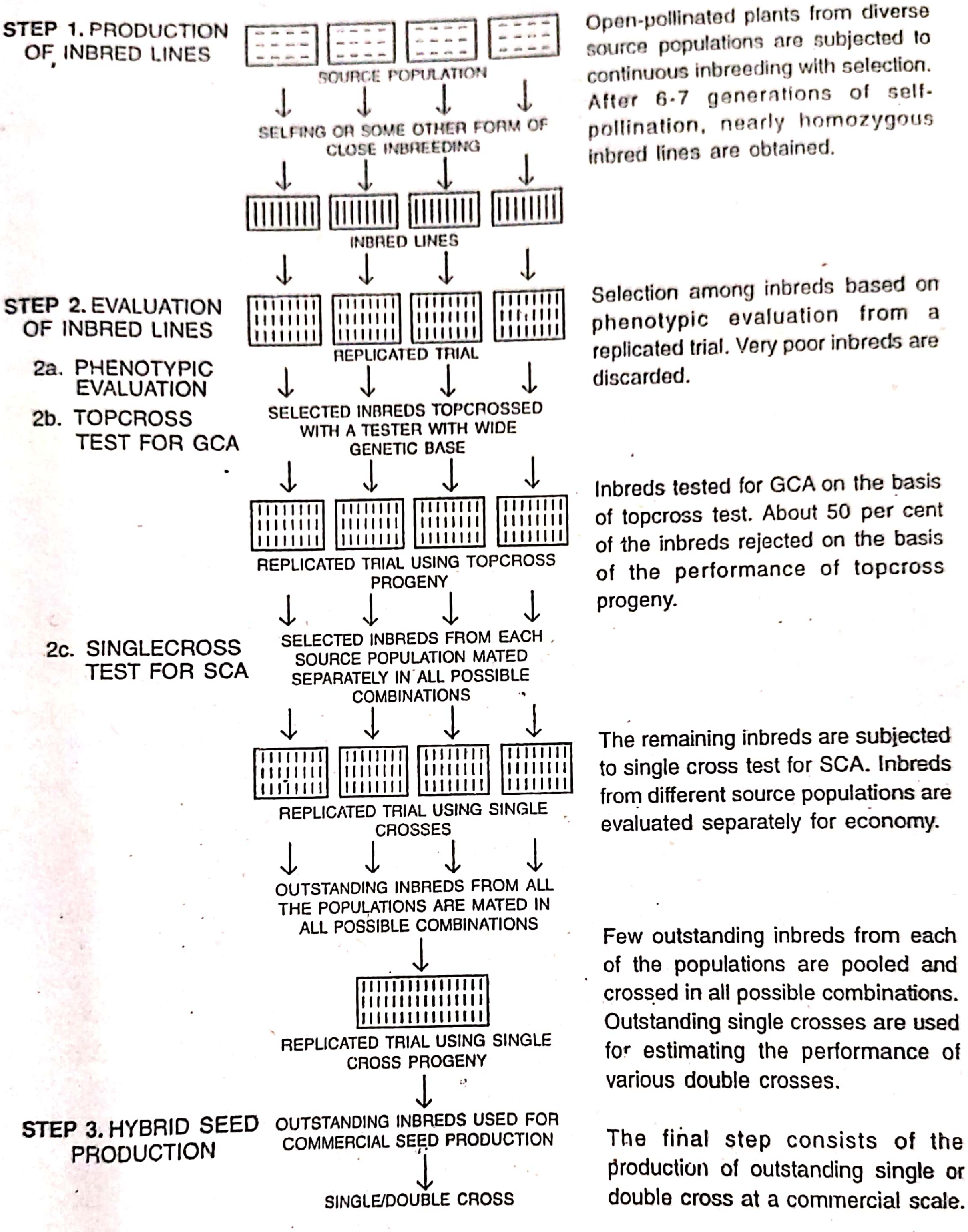

Fig. 22.1. Steps in the production of hybrid varieties in cross-pollinated crops; based on the present practice in maize.

variety, which may or may not have been subjected to population improvement, are known as ***first cycle inbreds.*** On the other hand, inbreds isolated from hybrid varieties are termed as ***second, third*** or ***fourth cycle inbreds*** depending upon the number of improvement cycles (0, 1 and 2, respectively) the inbreds making-up the hybrid varieties have been subjected to. The inbreds isolated from a synthetic variety may or may not be second cycle inbreds. This is because if the synthetic variety were derived from inbreds, the inbreds isolated from it would diallel manner to produce all possible single crosses (reciprocals are not included). In a ***diallel system of mating,*** each inbred is crossed with every other inbred. This produces *n* (*n* – 1) single crosses if the reciprocal crosses are also made, and *n* (*n* – 1)/2 single crosses if the reciprocals are ignored. The performance of single crosses is evaluated in a replicated yield trial, preferably over years and locations. Outstanding single crosses are identified and may be released as hybrid varieties where production of single cross seed is commercially feasible. More commonly, *e.g.*, in the case of maize in India, the performance of single crosses is used to predict the performance of double crosses.

22.5.4. Prediction of Double Cross Performance

Prediction of double cross performance form the data on single crosses is a widely accepted practice. This method was developed by Jenkins in 1934 after he evaluated the predictions based on the performance of inbred lines, single crosses and topcrosses. Not only this saves enormous time, labour and money, it is surprisingly accurate. *The predicted performance of any double cross is the average performance of the four nonparental single crosses involving the four parental inbreds.* Suppose, we wish to predict the performance of a double cross involving the four inbreds A, B, C and D. The six possible single crosses among these inbreds would be A × B, A × C, A × D, B × C, B × D and C × D. These single crosses can be combined to produce 3 double crosses, *viz.*, (A × B) × (C × D), (A × C) × (B × D) and (A × D) × (B × C). The performance of any of these double crosses can be predicted from the performance of the four single crosses that are not involved in producing that particular double cross. For example, the performance of double cross (A × B) × (C × D) would be the average of the performances of single crosses A × C, A × D, B × C and B × D, since these single crosses are not involved in producing this double cross. Similarly, the performance of double cross (A × C) × (B × D) can be predicted from the average of the performances of single crosses A × B, A × D, B × C and C × D. Which single crosses would be used to predict the performance of double cross (A × D) × (B × C) ? However, it may be pointed out that recent evidence suggests that the prediction based on performance of nonparental single crosses underestimates the performance of double and three-way crosses, and there is some risk of missing good parental hybrids (see, Banga and Banga, 1998).

The ***order of inbreds in a double cross*** is decided by their genetic relationship. Inbreds that are genetically related, *i.e.*, derived from the same source or related sources, are used to produce the single crosses. Genetically unrelated single crosses are then mated to produce the double cross. For example, if inbreds A and B are from one source, while C and D are from another, A would be crossed with B, and C would be mated with D to produce the single crosses A × B and C × D. These single crosses would then be mated to produce the double cross (A × B) × (C × D); this would be the best double cross from these four inbreds.

22.6. PRODUCTION OF HYBRID SEED

The two requirements for commercial hybrid seed production are, (1) easy emasculation of the female parent, and (2) effective pollen dispersal from the male parent to ensure a satisfactory seed set in the female parent. Both these factors are largely governed by the floral structure and the natural mode of reproduction of the crop species in question. For example, emasculation in maize, due to its peculiarly favorable floral structure, consists of a very simple operation of ***detaselling***, *i.e.*, removal of the entire tassel (the male inflorescence) from the plant before pollen is shed. Thus one simple operation emasculates the whole plant. The production of hybrid maize till 1960s was essentially based on detasselling. However, male sterility and self-incompatibility offer the means for ***genetic emasculation***, that is, preventing self-fertilization by manipulating the genotype of a plant, and are the bases of hybrid seed production in many crops. Pollen dispersal is often satisfactory in most cross-pollinated species since it is their natural mode of reproduction. In self-pollinated species, however, satisfactory pollen dispersal is often the limiting factor in hybrid seed reproduction. Hybrid seed may be produced in one of the following several ways: use of (1) cytoplasmic-genetic male sterility, (2) cytoplasmic male sterility, (3) genetic male sterility (4) self-incompatibility, (5) pistillate condition, (6) chemically-induced male sterility, and (7) manual emasculation and/or pollination. The first six systems have been described in some detail in Chapters 5 and 6 where their merits and demerits have been discussed. The first and the seventh systems have been described in Chapter 19 in relation to jowar and cotton, respectively.