generated by the molecular mapping of the corn chromosomes. Transformation does not replace conventional breeding procedures, but it provides a new breeding tool whereby DNA may be inserted into the corn genome from a wider range of donors than is possible by traditional cross-fertilization procedures.

FLOWERING AND POLLINATION

The corn plant has *monoecious* flowering structures with *staminate* flowers borne in the tassel and *pistillate* flowers borne on a shoot midway of the stalk. Pollination is consummated by transfer of viable pollen from the staminate flowers in the tassel to the silks, the receptive organs of the pistillate flowers. Wind is the principal agent in the uncontrolled or *open-pollination* of the corn plant. Normally, about 95% of the ovules on a shoot are cross-pollinated and 5% self-pollinated. Most of the pollen that pollinates an ear of corn comes from plants in the immediate vicinity, although the pollen may be carried by the wind for great distances. It is not uncommon to observe occasional yellow grains in ears of white corn even though the nearest field of yellow corn from which the pollen could have originated was 1000 m distant.

The main stem of the corn plant terminates in a tassel which bears two-flowered staminate spikelets, each flower having three anthers (Fig. 17.2). As the tassel flower opens, the anthers are pushed out by elongating filaments (Fig. 17.3), and pollen grains are emptied from the extruded anthers. A single tassel from a normal plant may produce 25,000,000 pollen grains, or an average of over 25,000 pollen grains for each kernel on an ear of corn. Pollen shedding usually begins one to three days before the silks emerge from the shoots of the same plant and continues for three to four days after the silks on the plant become receptive to pollen. The pollen may be killed by temperatures above 35°C (95°F) during the pollination period. Considering the large number of pollen grains produced, seed set is normally unaffected if 10% of the pollen grains survive. In the breeding nursery where pollen supply may be limited, high temperatures can severely reduce seed set.

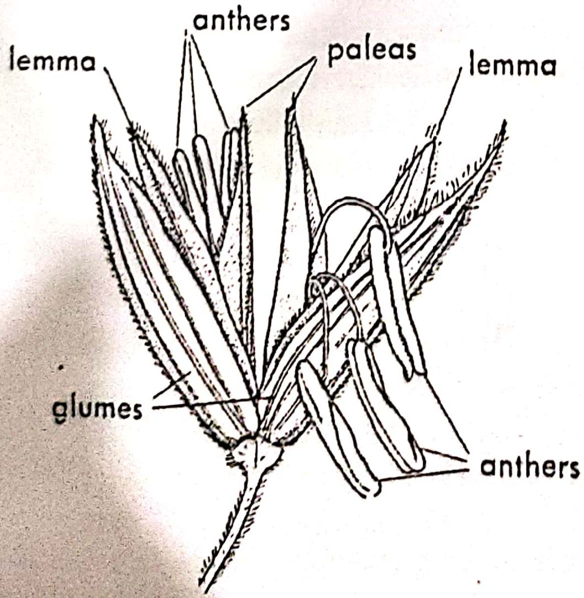

FIG. 17.2. Staminate spikelet of corn. Staminate spikelets are two-flowered, each with three anthers.

The ear shoots arise as branches from nodes about midway on the stalk. Each shoot is composed of a shank from which the husks arise and terminates in the cob on which the pistillate flowers are borne (Fig. 17.4A). The spikelets are borne in pairs, each spikelet normally containing one fertile and one sterile ovule, resulting in an even number of rows of kernels on the ear. Fertilization of the second ovule produces crowded and irregular rows of kernels on the ear. The silks are attached to the tip of the ovary (Fig. 17.4B). The silks function both as stigma and style and are receptive to fresh pollen throughout their entire length. Fertilization of the ovule usually occurs within 12 to 24 hours after the

FIG. 17.3. Tassel branch of corn with anthers exerted from a staminate flower.

silks have been pollinated. Severe drought delays emergence of the shoots, which combined with early termination of pollen shedding, will result in failure to set seed and in the production of barren or partially barren ears.

Xenia

Xenia is the immediate effect of pollen on the developing kernel. When yellow corn pollen fertilizes an ovule of white corn, a light-yellow kernel develops. When white corn pollen fertilizes an ovule of yellow corn, a medium yellow kernel develops. By cutting a kernel of yellow corn lengthwise it will be observed that the yellow color is found only in the vitreous starch of the endosperm, whereas the seedcoat is white or transparent. The endosperm develops from fusion of the second sperm nucleus with the diploid polar nuclei and has a triploid chromosome number. Yellow endosperm color is conditioned by a dominant gene (*Y*); the recessive alleles (*yy*) produce a white endosperm. Because the endosperm receives two sets of chromosomes from the polar nuclei, it will receive two genes for *Y*, or *y*, depending on the character of the mother plant, to one gene for *Y*, or *y*, from the pollen. Table 17.1 lists the possible combinations of endosperm color genes from the polar nuclei with endosperm color genes from the pollen and the xenia effect on endosperm color of the developing kernel. In addition to yellow vs. white endosperm color, endosperm characters that exhibit xenia are purple vs. colorless aleurone (Fig. 17.5A), starchy vs. sugary endosperm (Fig. 17.5B), nonshrunken vs. shrunken endosperm, and nonwaxy vs. waxy endosperm.

Table 17.1. Endosperm color genes and xenia effect in corn endosperm

Endosperm color genes in polar nuclei		Endosperm color genes in sperm		Endosperm color genes and xenia effect in endosperm
YY	+	*Y*	=	*YYY* (deep yellow)
YY	+	*y*	=	*YYy* (medium yellow)
yy	+	*Y*	=	*Yyy* (light yellow)
yy	+	*y*	=	*yyy* (white)

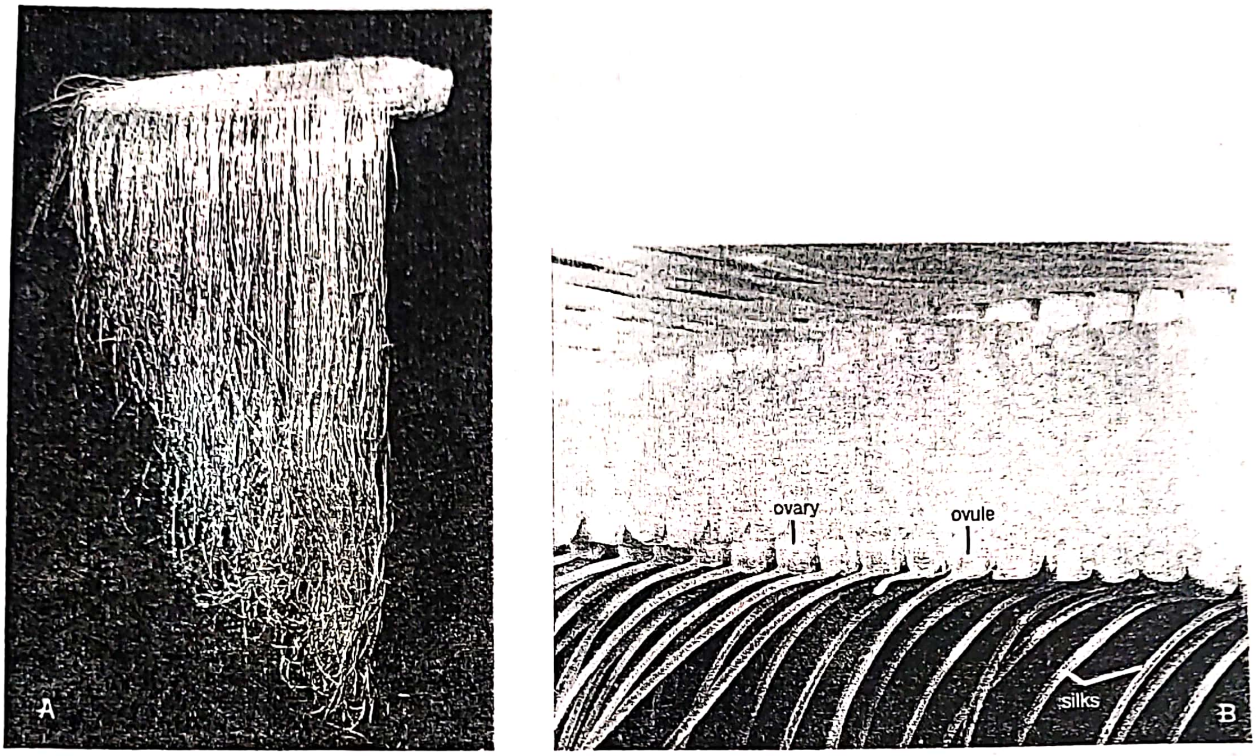

FIG. 17.4. Ear shoot of corn. (A) With husks removed. A fresh silk is receptive to pollen along its entire length. (B) Cross section of ear shoot showing silks attached to tip of the ovaries.

HETEROZYGOSITY OF OPEN-POLLINATED CORN

Heterozygosity and genetic variability are characteristics of cross-pollinated crops (Chapter 10). Conceivably, every ovule on an ear of open-pollinated corn could be pollinated by a different pollen parent; this makes it doubtful that any two seeds on an ear of corn, or any two plants in a field of open-pollinated corn, have exactly the same genotype. Each corn plant is a different hybrid genotype, and a field of open-pollinated corn is a mixture of complex hybrid plants with both genotypic and phenotypic variation (Fig. 11.1). With each new generation, there is a reshuffling of the genes, which keeps open-pollinated corn highly heterozygous and maintains its genetic variability.

BREEDING OPEN-POLLINATED CORN

Improvement in corn has taken place through selection by Native Americans since its earliest cultivation. Choosing an ear of corn for seed was an obvious practice that had to be repeated each time corn was planted. In the United States, many open-pollinated cultivars of dent corn were developed by farmer-breeders during the latter half of the nineteenth century.

Mass Selection

Mass selection as a breeding procedure is used to maintain existing open-pollinated cultivars and for developing new cultivars. In the mass selection method of breeding open-

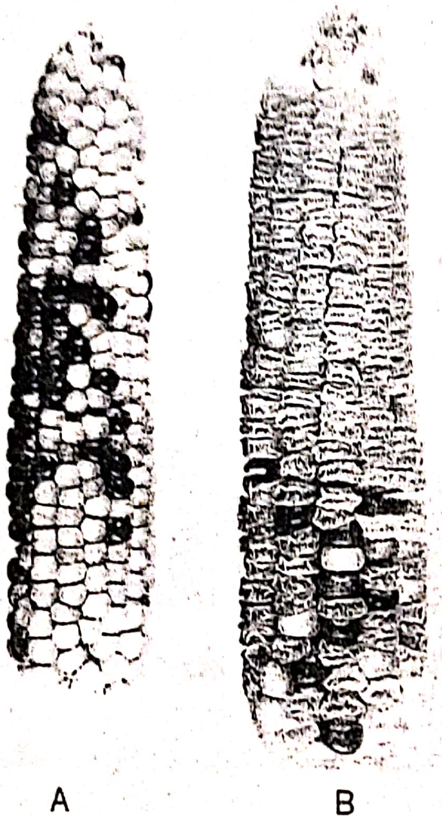

FIG. 17.5. Xenia in corn. (A) White corn partly pollinated from purple corn. (B) White, sugary endosperm corn partly pollinated from white and purple, nonsugary-endosperm field corn.

pollinated corn, ears are chosen on the basis of visible plant and ear characteristics. Seeds shelled from the ears are mixed and planted en masse. Mass selection is a form of recurrent selection with the plant as the unit of selection and with selection repeated each generation. New variety types of open-pollinated corn were developed for new production areas, such as the early dents for the northern Corn Belt, or for specific purposes, such as large, woody cobs for making cob pipes. Each farmer became a breeder as he selected ears for planting the next year's crop. By repeated selection the farmer-breeder could change the appearance of the corn plant for visible characteristics such as height, maturity, or ear and kernel conformation. Selection was often based on ear and kernel types that would win prizes in a corn show, or just to suit the fancy of the breeder, without knowledge of the effect that the selection would have on performance. Although the physical appearances of the open-pollinated cultivars were changed by mass selection, yield was not significantly improved because:

- selection was based on visible characters of the plant generally unrelated to yield,
- superior plants were pollinated at random with pollen from both superior and inferior yielding plants, and
- rigorous selection for specific plant characteristics often led to inbreeding and a decrease in vigor.

It has since been demonstrated that mass selection can be effective in improving yield if grain weight rather than unrelated visual features is the primary selection objective and if experimental procedures are followed that reduce the effect of the environmental variation on selection. The latter was accomplished by subdividing the experimental area into small *subplots* or *grids*. Each subplot was harvested separately, and only the heaviest ear from each subplot was retained for planting the next generation. Beginning in the 1930s, mass selection was discontinued as a breeding procedure in the United States but is still used in underdeveloped countries.

Ear-to-Row Breeding

The ear-to-row breeding method was first used by C.G. Hopkins at the Illinois Agricultural Experiment Station about 1896 in selection experiments to increase protein and oil content in corn. The essential features of the ear-to-row system of breeding, as it later developed, are as follows:

- fifty to 100 ears are shelled separately with part of the seed from each ear planted, an ear to a row; remnant seed from each ear is labeled and stored separately,
- each row is scored for desirable characters and harvested for yield so that the superior rows may be identified, and
- remnant seed lots from superior rows are mixed and used to plant an open-pollinated plot the second year, from which ears are selected for repeating the process.

Visual plant and kernel characters could be altered with the ear-to-row method of breeding in the same manner as with mass selection, but the changes occurred more rapidly because the pollen source was controlled and limited to selected genotypes. For characters such as yield that are not evaluated accurately by visual observation, the method was ineffective for the same reasons that mass selection was ineffective. By modifying the procedure to include replication, so that environmental effects on yield could be separated from genetic effects, yield could be altered by ear-to-row selection. The ear-to-row procedure is the same as the procedure described in Chapter 10 as 'half-sib with progeny test.'

Variety Hybridization

Hybridization between open-pollinated cultivars of corn, either intentional or accidental, was responsible for the origin of many of the commercial cultivars of open-pollinated corn. In 1880, W.F. Beal at the Michigan Agricultural Experiment Station described a variety hybridization experiment in which a cultivar of open-pollinated corn was detasseled and pollinated by a second cultivar growing in an adjacent row. An increase in yield was obtained when seeds harvested from the detasseled row were planted. Beal described a procedure by which farmers could produce their own crossed seed that closely resembles present hybrid seed production procedures. But the technology was too advanced for that period and variety hybridization never became popular with farmers.

HYBRID CORN

Corn became the model for breeding hybrid cultivars. The double-cross hybrid, proposed by D.F. Jones in 1918, became the model for breeding hybrid corn until replaced by the single-cross hybrid in the 1960s. During the 1920s and 1930s, major efforts in breeding hybrid corn were directed toward development of inbred lines from open-pollinated cultivars and fitting the inbred lines into productive single- and double-cross hybrid combinations adapted to the United States Corn Belt. This effort, led by F.D. Richey for the United States Department of Agriculture, H.K. Hayes in Minnesota, M.T. Jenkins and G.F. Sprague in Iowa, and many other corn breeders, was dedicated to finding the most efficient procedures for breeding hybrids. By the 1940s hybrid corn had replaced most of the open-pollinated corn throughout the United States Corn Belt and was being introduced to other major corn producing areas of the world.

The 1950s and 1960s brought innovations that further changed corn hybrid seed production practices:

- introduction of cytoplasmic male-sterility (cms) to eliminate detasseling, and
- replacement of double-cross hybrids with productive single-cross hybrids.

Until the concept of hybrid corn, there was no breeding method by which every plant within a field of corn would be a high-yielding genotype. Additionally, the breeder's ability to identify the high yielding plants was limited because procedures for field-plot testing and data analyses available at that time did not permit separation of genetic and environmental effects on yield. For hybrid corn to be widely grown, it was also necessary that the hybrid seed be available at prices that the farmer could afford. To meet this need private seed companies emerged to produce and market the hybrid seed. Most of the seed companies developed extensive breeding and research programs, and, over time, the breeding of hybrid cultivars of corn passed from the publicly supported breeding programs to the private breeding programs.

What Is Hybrid Corn?

Hybrid corn is the first-generation progeny from a cross between inbred lines or hybrids among them. The double-cross hybrid has been replaced by the single-cross hybrid, modified single-cross hybrid, and three-way cross combinations. All are based on the farmer growing F_1 populations of crosses among homozygous inbred lines.

INBRED LINES. Inbred lines of corn are populations of identical (or nearly identical) homozygous plants usually developed by self-pollination. Inbred lines are (*a*) the products from inbreeding heterozygous plants from open-pollinated populations until homozygosity is reached or (*b*) products from inbreeding segregating populations following a cross between two inbred lines. The latter is comparable to the hybridization procedure in breeding self-pollinated species. In producing inbred lines in corn, pollination is controlled, as illustrated in Figure 17.6A to 17.6F.

SINGLE-CROSSES. A single-cross is the hybrid progeny from a pollination between two homozygous inbred lines (Fig. 17.7). Single-cross plants are heterozygous at all loci in which the parent inbreds differ; yet, within the single-cross, plants are genetically identical (or nearly identical). In the farmer's field, the single-cross hybrid is uniform in appearance, maturity, and yield potential; yet it exhibits vigor and productiveness that was lost during inbreeding. The combinations of inbred lines that may be crossed to produce superior-yielding single-crosses are rather rare. So new inbred lines are tested for general and specific combining ability (gca and sca) to identify productive single-cross combinations (see Chapter 11). Modern inbreds are more vigorous and productive than those developed earlier, and kernel size and shape approach that of hybrids. These improvements made it possible for seed producers to market and the farmer to grow single-cross corn hybrids.

In the commercial production of single-cross hybrid seed, the parent inbreds are planted in separate rows in an isolated field. Choice of inbred to be used as the pollen parent, and inbred to be used as the seed parent, will generally be determined by which inbred produces the most plentiful supply of pollen and which inbred produces the largest yield of seed. A planting pattern in common use for single-cross hybrid seed production is to plant one pollen-parent row to four seed-parent rows (ratio 1:4) (Fig. 17.8). In this arrangement, one-half of

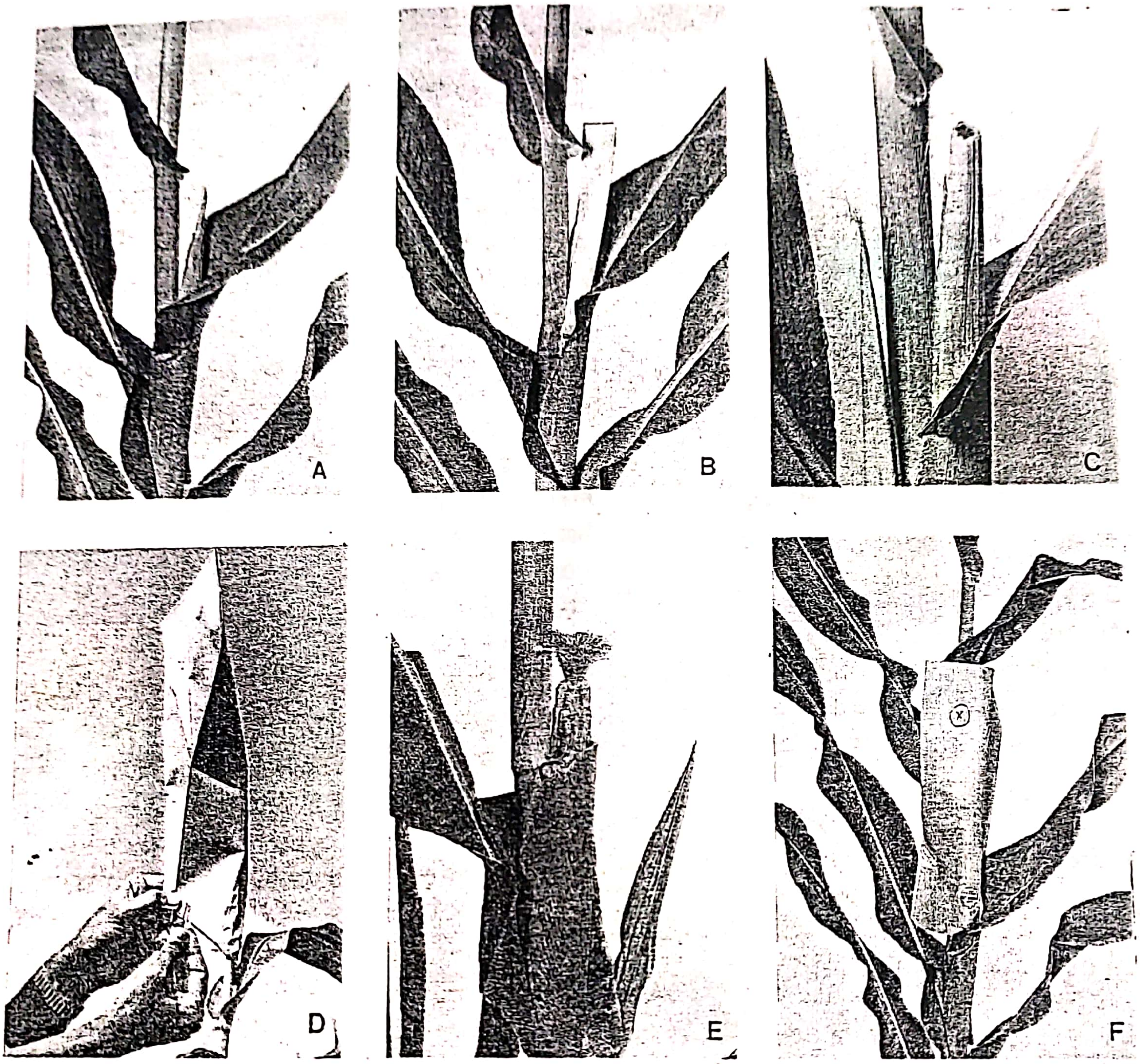

FIG. 17.6. Steps in selfing and crossing corn. (A) Ear shoot of corn emerging from the leaf sheath. Ear shoots are covered 1 to 2 days before the silks emerge to prevent their being pollinated. (B) A parchment ear shoot bag has been slipped over the ear shoot. (C) The ear shoot is cut back on the day before pollination and the shoot bag replaced immediately. (D) A tassel bag is fastened over the tassel on the day before the pollen is to be collected. (E) Silk brush grown out ready for pollination. The brush provides a uniform growth of fresh silks on which to distribute the pollen. (F) After pollination of the brush, the tassel bag is fastened over the shoot to protect the developing ear.

the seed-parent rows are adjacent to a pollen-parent row, and none are more than two rows from the pollen parent. The seed-parent rows are detasseled and pollinated by wind-blown pollen from the adjacent pollinator parent. The pollen-parent row is destroyed after pollination to prevent seed mixture during harvest. The pedigree of a single-cross made from inbreds **A** and **B** is written **A** × **B** where **A** is the seed parent and **B** is the pollen parent.

MODIFIED SINGLE-CROSSES. A modified single-cross is the hybrid progeny from a three-way cross, which utilizes the single-cross from crossing two related inbreds as the seed parent and an unrelated inbred as the pollen parent (Fig. 17.9). The two related inbred lines (**A′** and

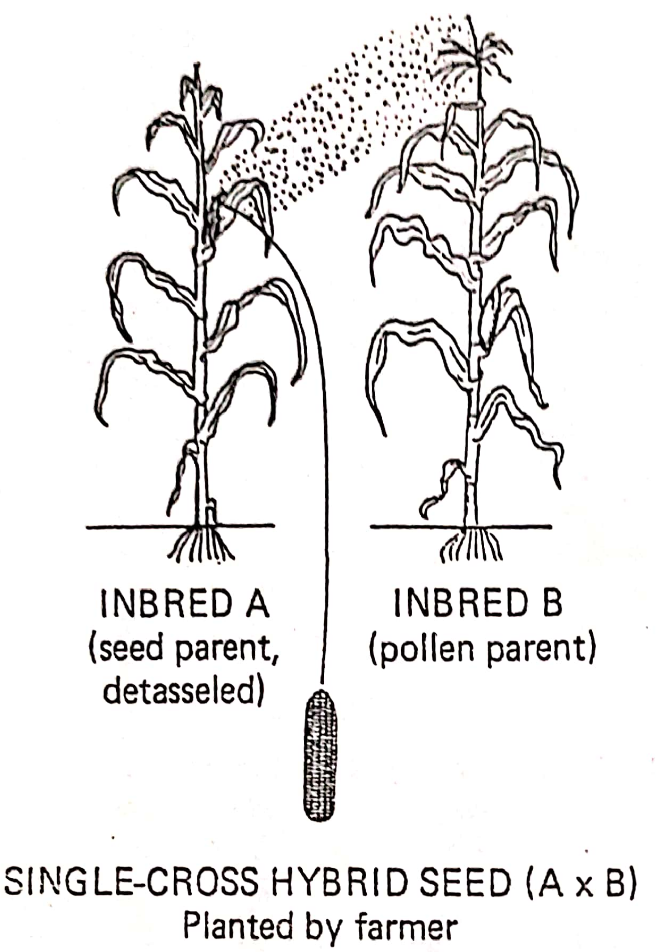

FIG. 17.7. Procedure for making single-cross hybrid corn. The seed parent, inbred A, is detasseled and pollinated from the pollen parent, inbred B.

A") are genetically similar with respect to plant type but genetically different to the extent that when crossed heterosis for vigor and yield is expressed. This type of hybrid has the advantage of a single-cross hybrid in the farmer's field and that of a three-way cross in seed production. The pedigree of a modified single-cross made with inbreds **A′**, **A″**, and **B** is written (**A′** × **A″**) × **B**.

THREE-WAY CROSSES. A three-way cross is the progeny from a cross between a single-cross hybrid and a third inbred line. The three-way cross differs from the modified single-cross in that all three inbreds are unrelated and the hybrid progeny will be more diverse genetically and less uniform, but it has the advantage that the seed is produced on a single-cross instead of an inbred line. The pedigree of a three-way cross made with the single-cross (**A** × **B**) and the inbred **C** is written (**A** × **B**) × **C**.

DOUBLE-CROSSES. A double-cross is the hybrid progeny from a cross between four unrelated inbreds. The inbreds are crossed in pairs to produce two single-crosses, which are then crossed to produce the double-cross. The pedigree of a double-cross made with inbreds **A**, **B**, **C**, and **D** is written (**A** × **B**) × (**C** × **D**).

TOP CROSSES. A *top cross* (also called an *inbred-variety cross*) is made by pollinating an inbred line or single-cross with pollen from a genetically mixed population.

MULTIPLE CROSS. A multiple cross is the product of any combination of crosses using more than four inbreds.

Cytoplasmic Male Sterility in Hybrid Seed Production

Prior to the 1950s, hybrid seed corn was produced by the conventional procedure of alternately planting rows of seed-producing and pollinator parents and detasseling the seed-producing (female) parent rows, which would then be pollinated from the pollinator (male) parent rows. During the 1950s, a cytoplasmic-male sterile, fertility-restorer gene system was introduced that replaced detasseling in the production of hybrid seed corn. The male-sterile cytoplasm then used was obtained from the open-pollinated cultivar 'Mexican June' and became known as the Texas-type cytoplasm, or **cms-T**. Fertility was restored by restorer genes Rf_1 and Rf_2 and additional modifier genes. The cms and the fertility restorer genes were introduced into the inbreds by a series of backcrosses (Chapter 11).

FIG. 17.8. Commercial seed-production field of single-cross hybrid corn planted in a ratio of 1 male pollinator row to 4 female seed-parent (detasseled) rows. With this planting pattern, one-half of the seed-parent rows are separated from a pollen-parent by only one row. Additional pollinator rows are planted at the edge of the seed-production field to provide for pollen saturation and ensure genetic purity. Soybean planted at the left of the field provides additional isolation as required for hybrid seed production.

In 1970, a corn leaf blight disease incited by the pathogen *Bipolaris maydis* (Nisik.) Shoem. (Syn. *Helminthosporium maydis* Nisik. and Miyake) spread through the Corn Belt. The pathogen was virulent on corn hybrids with the cms-T cytoplasm. Because more than 90% of the hybrid corn being grown in the United States at that time contained the cms-T cytoplasm, damage from the leaf blight disease was extensive. As a result of this experience, the utilization of the cytoplasmic-male sterile:fertility-restorer gene system to eliminate detasseling in corn was discontinued. Producers of hybrid seed corn then returned to detasseling in hybrid seed production.

BREEDING IMPROVED HYBRIDS

A new era in plant breeding was ushered in with G.H. Shull's proposal in 1909 for *A Pure Line Method in Corn Breeding*, in which the object would be "not to find the best pure line, but to find and maintain the best hybrid combination." Discovering efficient procedures for finding and maintaining superior hybrid combinations has occupied the attention of corn breeders ever since. In the beginning, as farmers changed from open-pollinated cultivars to