Maize (Zea mays L.) ranks with wheat (Triticum spp.) and rice (Oryza spp.) as one of three most important cereal crops in the world. In terms of total global production, maize normally exceeds 400 million metric tons (Mt) per year, compared with almost 500 Mt for wheat and just under 400 Mt for rice. Maize is cultivated in a wider range of environments than either wheat or rice because of its greater adaptability. During the past decade, global maize production has increased about 140 Mt. This represents a 3.1% annual increase in yield improvement and a 1% per year expansion in the area of maize cultivation.

The four major uses of maize are for livestock feed, human consumption, industrial purposes, and seed. Globally, 67% of the maize is used for livestock feed, 25% for human consumption and industrial purposes, and the balance is either used for seed or is lost in wastage. Historically, maize has been primarily used for livestock feed in developed countries, with greater human consumption in developing countries. Use of maize as feed for livestock production has increased more rapidly than for direct human consumption in the developing countries during the past decade.

TYPES OF CULTIVARS

Mode of Propagation

Maize is a monoecious plant with separate male and female flowers on the same plant. The male flowers are located at the top of the plants in the tassel, and the female flowers are located about midway up the stalk in the ear shoot (Fig. 8-1). Because maize has separate male and female flowers,
cross-pollination is the normal method of reproduction. Pollen grains are dispersed by wind currents, and it is estimated that under natural conditions, cross-pollination is greater than 99%. The male flowers usually mature before the female flowers. The difference in maturity of the male and female flowers depends on the genotypes and the environmental conditions at the time of flowering. Stress conditions caused by heat and drought hasten the maturity of male flowers and delay maturity of female flowers. In extreme conditions of high temperatures of about 35 to 40°C and moisture stress, male flowers may not produce fertile gametes and female flowers may not emerge for pollination. Damage of male flowers due to environmental stress is usually referred to as tassel blasting and damage of female flowers causes barrenness.

When the male flowers are mature, anthers are exerted from the spikelets on the tassel, and pollen is dispersed through a pore at the end of the anther. Anther exsertion on the tassel usually begins a short distance below the top of the tassel and progresses up and down the tassel as it matures. Pollen from the anthers maybe dispersed in only a few minutes, or over a greater period depending on the plants' genotype and on environmental conditions. Pollen shed for a tassel may occur during only 1 or 2
days or for as long as a week or more, depending on genotype and environment. The number of pollen grains dispersed by a tassel depends on the genotype and vigor of the plants. Hybrids will shed more pollen for a longer period than inbred lines. It is estimated that a tassel produces 25,000 pollen grains for each female gamete in a normal environment (Kiesselbach, 1949). The timing of pollen shed during the day varies with the genotypes and environment. It may begin 3 hours after sunrise on warm days with no dew and continue for 1 to 3 hours. If the morning temperatures are cool, pollen dispersal may be delayed until midday and continue most of the afternoon. After the pollen has been released and dispersed, it remains viable for only a few minutes.

Maize has the potential for more than one female flower (ear shoot) per plant, and the number of ear shoots per plant varies among cultivars. Because of past selection, the top ear shoot usually is located at the sixth or seventh node below the tassel in U.S. Corn Belt cultivars. There is an axillary bud at each node below the top ear shoot; hence, there is the potential for an ear shoot to develop at each node below the top one. Although selection for development of only one ear has been relaxed in recent years, ear development usually occurs at only the top two or three ear-bearing nodes. Ear shoots include two visible structures: (a) modified leaves, usually called husks, that envelop the cob, and (b) silks that emerge from the end of the cob and husks [Fig. 8-1(b)]. The silks that emerge from the tip of the cob are functional stigmas; one stigma for each potential kernel. Silk emergence progresses from the base to the tip of the cob. Silk emergence is usually later than pollen shed, and the interval between pollen shed and silk emergence depends on the cultivar and the environmental conditions at flowering. If the plants have silks expressed on more than one ear shoot, silks usually emerge a few hours or 1 or 2 days earlier on the top ear shoot than on the second or third. Under optimum conditions of cool temperatures and high humidity, silk emergence may be completed in 2 to 3 days and be coincident with pollen shed. Under extreme stress conditions of high temperatures of 35 to 40°C and poor moisture availability, silk growth may cease and not be available for fertilization at the time of pollen shed. If the conditions for producing viable male and female gametes are not satisfactory, the mature ear shoots may have either no kernels or a scattered seed set. Poor seed set may be due to non-viable pollen or silks, or to poor synchronization of the time of pollen shed and silk emergence.

Under natural field conditions, fertilization is accomplished by random pollination because pollen grains are circulated by wind currents. Pollen grains come in contact with the silks, grow down the styles, and unite with the female gametes. Double fertilization in the embryo sac results in the formation of the embryo (2n = 20) and the endosperm (3n = 30) of the seed.
Past and Current Cultivar Types

The types of maize cultivars available to farmers, breeders, and geneticists have changed rapidly the past 60 years. Because maize is a cross-pollinated species, it was propagated as open-pollinated cultivars by the early farmers and breeders. Each cultivar was a collection of individuals that were heterozygous and heterogeneous. Although there was usually a range of variability within each cultivar, each one was distinctive for several different traits.

Maize is grown from 58° north latitude without interruption through the temperate, subtropical, and tropical regions to 40° south latitude; from sea level to elevations over 3800 m; and in areas with less than 25 cm of rainfall to more than 1020 cm. Consequently, many distinctive cultivars were developed for each ecological niche. Natural selection in the environments where the cultivars were grown was effective for developing strains that had pest resistance, could germinate and grow in cool temperatures at high elevations, had drought and heat tolerance, and could mature in short growing seasons at higher latitudes. Most of these traits have a complex inheritance, and their genetic basis is not well understood in most instances. Within each ecological niche, cultivars were developed that met specific needs of the early civilizations. Selection was imposed by humans, primarily by visual selection for traits considered important locally, such as seed color and texture.

Both environmental and human selection played important roles in the development of the landrace cultivars available when the European colonists arrived in the Western Hemisphere. Extensive collections of maize cultivars in the region suggested that as many as 250 to 300 races of maize existed (Goodman, 1985). Because of overlap between different regions, it seems that 150 distinctive races are more nearly correct.

Most of the maize germplasm in the United States was derived from Corn Belt Dents, a race formed by intercrossing the early, long-eared Northern Flints and the late, white Southern Dents. The Corn Belt Dents are a relatively new race that arose primarily in the nineteenth century. Either planned or accidental crosses were produced between the Northern Flints and Southern Dents as the colonists expanded along the eastern seaboard and into the eastern part of the U.S. Corn Belt. Selection gave rise to cultivars adapted to specific niches. Some cultivars, such as ‘Reid Yellow Dent,’ became widely distributed, and substrains developed by specific individuals became available. Until the twentieth century, however, only open-pollinated cultivars were available.

The number of open-pollinated cultivars available in the United States is not known. Unfortunately, many cultivars were lost and not maintained before it was realized that they were important sources of germplasm for
breeding programs. Extensive selection had been conducted by individual farmers and seedsmen to develop specific cultivars. Selection within open-pollinated cultivars also was stimulated by the maize contests and shows that emphasized specific traits that conformed to scorecard standards. The effectiveness of selection by specific traits and the relationship of scorecard standards to performance were minimal (Hallauer and Miranda, 1981).

Although extensive selection within open-pollinated cultivars had been conducted in the United States during the nineteenth century and first two decades of the twentieth century, there was very little change in performance (Fig. 8-2). From 1875 to 1935, there were only 2 years when yields exceeded 20 quintals per hectare (q/ha). During the 1930s, there was a tremendous change in the types of cultivars available for U.S. farmers. Based on studies conducted by Shull (1909) and the suggestion of Jones (1918), the inbred-hybrid concept was developed and exploited to produce double-cross hybrids. Replacement of the open-pollinated landrace cultivars by double-cross hybrids resulted in a rapid advance in productivity (Fig. 8-2). The new double-cross hybrids had greater yields, greater stability of yields, better standability, and more uniform maturity than the open-pollinated cultivars. Nearly 100% of the hectarage in Iowa and Illinois was planted to double-cross hybrids by 1945, and they

Figure 8-2  Average national maize yields in the United States from 1875 to 1985.
were used for essentially all the U.S. maize production by 1960. The inbred-hybrid concept of breeding dominated maize breeding programs after the 1920s. The experience with double-cross hybrids in the United States spread rapidly in other developed countries. During the 1960s, methods of pest control and production techniques were available to permit the commercial use of single-cross hybrids. Since the 1960s, single-cross hybrids have rapidly replaced double-cross hybrids in the United States. It is estimated that nearly 90% of the maize hybrids currently grown in the United States are single crosses.

In other advanced maize production areas of the world, hybrids predominate, but either double-cross or three-way crosses are used more commonly than single crosses. The extent of hybrid usage in other countries depends on the development of the support services necessary for the production and distribution of consistently good quality seed. In the lesser developed areas, improved open-pollinated cultivars are still used, although synthetic cultivars and synthetic-cultivar crosses are available. It seems, however, that some type of hybrid will be used in all maize-producing areas in the near future.

EXTENT AND NATURE OF BREEDING PROGRAMS IN NORTH AMERICA

Public Programs

Public maize breeding programs have existed for nearly 100 years, but the nature and extent of these programs have changed significantly during this time. Beal (1877) produced and tested cultivar crosses in Michigan. His studies were the first to report on the heterosis expressed in crosses of cultivars. However, the studies did not have much impact, and crosses of open-pollinated cultivars were never used to any extent in the United States. Modern maize breeding was based on the inbred-hybrid concept described by Shull (1909).

Maize breeding in the public sector changed dramatically in the 1920s. Because of the vision and foresight of some individuals on the potential of the tenets suggested by Shull, maize breeding programs were initiated and expanded throughout the United States. The major research thrust of all programs was to exploit the potential of developing inbred lines for use in hybrids. The U.S. Department of Agriculture (USDA) rapidly expanded its efforts in maize breeding in 1922, many in cooperation with the State Agriculture Experiment Stations. Research conducted by the USDA and the State Agriculture Experiment Stations included all aspects of maize improvement, but major emphasis was related to developing and testing double-cross hybrids. About equal emphasis was given to
basic and applied research, although the proportion varied among individuals and research programs.

Breeding programs in the public sector continued to be prominent until the 1960s. Basic research was conducted to determine the most effective and efficient methods of inbred line development, evaluation of inbred lines for potential worth in hybrids, and plot techniques and methods for evaluation of hybrids. Methods of inbred line development and hybrid evaluation were well established by the 1940s for production of double-cross hybrids. There was concern, however, that adequate genetic variability was not available for continued progress and that the types of gene action exploited in hybrids was nonadditive (Hull, 1945). Additional types of research were initiated in the public sector for evaluating methods of germplasm enhancement and types of gene action operative in maize populations and hybrids. Extensive theoretical and empirical studies were conducted relative to the inheritance of quantitative traits, recurrent selection methods, and types of gene action responsive to different selection methods. Basic information obtained in these areas of research was applied to breeding programs that emphasized inbred line and hybrid development.

The first series of inbred lines and hybrids developed arose from breeding programs conducted in the public sector. Hybrids were tested and information made available to the public. It became obvious that the best hybrids were superior to the open-pollinated landrace cultivars grown by the farmers, particularly during the harsh environments experienced in the mid-1930s. When it became evident that there was a market for the hybrid seed, private organizations were formed to produce the hybrids developed by the public breeding programs. This trend continued until private companies had the available capital to conduct their own research programs. Although private companies were organized in the 1930s, it was not until the 1940s and 1950s that they initiated extensive research programs for inbred line and hybrid development. As a result of increased research by the private sector, there was a redirection of the public breeding programs. Less emphasis was placed on inbred line and hybrid development and greater emphasis was placed on basic research, graduate-student training, and teaching.

**Private Programs**

The market potential of maize hybrids was recognized by a few visionary entrepreneurs in the 1930s. Their primary goal was to take the lines and hybrids developed by public breeding programs and translate these into marketable products. After the techniques of seed production and marketing were developed, private organizations had the necessary capital to
initiate breeding programs for development of proprietary lines and hybrids. Although a few private breeding programs were conducted during the 1930s and 1940s, rapid expansion occurred during the 1950s and 1960s. The extent and nature of the breeding programs also changed during the 1950s and 1960s. In addition to the development of proprietary lines and hybrids, basic research was conducted relative to breeding methodology, germplasm enhancement, and exotic germplasm. The basic research studies were conducted to enhance the applied aspects of their programs.

During the last two decades, private investment has increased rapidly, both in the number of private organizations involved and in the extent of programs within individual organizations. Because of the economic returns expected from superior hybrids, sophisticated applied breeding programs have evolved to develop superior inbred lines and hybrids. The extent of modern, private breeding programs exceeds those in the public sector, either in the past or at the present. Resources have been allotted for extensive breeding nurseries and testing programs to evaluate large numbers of lines and hybrids. In recent years, private programs also have been developed in areas that were considered previously as fringe areas of maize production. Programs have been established in northern areas of the United States and southern Canada for early maturity hybrids, in the southern areas of the United States for full-season and short-season hybrids, and in the western part of the U.S. Corn Belt for hybrids that can tolerate hot, dry conditions. In all instances, efforts are being made to identify lines and hybrids that respond to specific environmental niches. Stability of hybrid performance is essential. Greater emphasis is given to pest resistance to reduce the fluctuations of hybrid performance.

The dependence of private firms on inbred lines and hybrids developed in public programs has steadily decreased. It is likely that this trend will continue in the future. Nevertheless, inbred lines are still released from public breeding programs and smaller firms that do not have resources to conduct their own breeding and testing programs depend on these materials. How long this situation will continue in the future is not clear.

Breeding programs in the private sector are very dynamic at present. Several factors are contributing to the changes: the reduction of investment in public breeding programs; chemical firms expanding into the seed business to expand their product line and service to farmers; development of biotechnological firms that desire to market products to maintain a cash flow; and expansion of established hybrid maize seed firms to remain competitive. Because of the competitive nature of the firms to acquire a market share of a $1.5 billion business, highly qualified researchers are recruited to conduct the research. Although primary emphasis is given to
product development, extensive basic research also is conducted to support product development. It seems, therefore, that publicly supported breeding programs will have reduced impact on hybrids grown by farmers in the future. Each firm producing and selling hybrid seed will have a self-contained research program.

BREEDING OBJECTIVES FOR CULTIVAR DEVELOPMENT

Priority of Characters and Results of Genetic Improvement

Grain yield is the most important economic trait and has always received major attention in maize breeding programs. Direct selection is emphasized for grain yield, but both direct and indirect selection for other traits can affect yield. Cultivars also must have acceptable levels of root and stalk lodging resistance and uniform maturity for mechanical harvesting. Direct selection for grain yield per se is more effective than when constraints are imposed for standards of other traits. Direct selection for grain yield in open-pollinated cultivars was not effective; however, selection was confounded with poor experimental techniques (Fig. 8-2). With improved experimental techniques, grain yield per se has been improved. Direct selection for grain yield per se is more effective than when constraints are imposed for standards of other traits considered important for modern production systems.

Traits other than yield that are considered important by maize breeders vary among breeding programs because of differences in the environment for which a hybrid is being developed. Resistance to stalk damage caused by the southwestern maize borer (Diatraea grandiosella) is very important in the southern United States, but of minor importance in Minnesota because the insect does not overwinter in the northern areas of the United States. Good root development is emphasized in the western part of the U. S. Corn Belt to withstand the effects of maize rootworms (Diabrotica spp.), drought stress, and strong wind currents. Damage due to virus infection is important in the eastern part of the U. S. Corn Belt. Cultivars that can emerge and grow under cool conditions in the spring and have rapid moisture loss in the fall are important traits in Minnesota, but they are not as important in Georgia. Recently, it has been determined that the incidence of eyespot (Kabatiella zeae), gray leaf spot (Cercospora zeae-maydis), and anthracnose (Colletotrichum graminicola) are greater problems with use of reduced tillage systems than on the fall-plow tillage system. Breeders, therefore, place different emphasis on traits in different environments.

Surveys conducted by Hallauer (1979) and Bauman (1981) documented the traits considered important in U.S. maize breeding programs
Table 8-1  Relative Importance of Traits in Maize Breeding Programs for Cultivar Development

<table>
<thead>
<tr>
<th>Trait</th>
<th>Ratings of Bauman (1981)*</th>
<th>Relative Importance in Future (Hallauer, 1979)†</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Importance Of Trait</td>
<td>Effectiveness of Visual Selection</td>
</tr>
<tr>
<td>Grain yield</td>
<td>1.2</td>
<td>3.2</td>
</tr>
<tr>
<td>Pest resistance</td>
<td>1.9</td>
<td>2.2</td>
</tr>
<tr>
<td>Maturity</td>
<td>1.9</td>
<td>1.5</td>
</tr>
<tr>
<td>Plant color</td>
<td>3.2</td>
<td>1.5</td>
</tr>
<tr>
<td>Plant and ear height</td>
<td>2.2</td>
<td>1.5</td>
</tr>
<tr>
<td>General plant</td>
<td>2.3</td>
<td>1.8</td>
</tr>
<tr>
<td>appearance</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Cold tolerance</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Efficiency N use</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Pesticide tolerance</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

*Ratings range from 1 to 4, where 1 indicates an important trait or that visual selection was effective; 4 indicates a trait of minor importance or that visual selection was ineffective.
†Percentage of individuals that indicated relative importance of trait.

(Table 8-1). Both surveys included breeders of public and private programs, but Hallauer found there were no differences between them. Bauman’s survey was for the present time, whereas Hallauer’s survey was for characters that breeders would consider important in the next decade. Grain yield was considered of greatest importance and would receive the same or greater attention in the future. Pest resistance and maturity also were important traits and would receive greater attention in the future. These traits are receiving greater emphasis because of expansion of maize production in areas with shorter growing seasons, double cropping in southern areas, and increased use of conservation tillage practices. Except for changes of emphasis in selection, most of the traits listed in Table 8-1 have received attention in most breeding programs.

Yield improvements for maize since the mid 1930s included a combination of factors: change from open-pollinated cultivars to hybrids; development of newer hybrids; and better management, equipment, and cultural practices for maize production. The trend for greater yields since the mid-1930s, therefore, includes both genetic and husbandry improvements. Studies have been conducted that permit the separation of genetic and environmental effects and determine their relative impact on yield improvement of maize since the 1930s. Most of the studies were patterned after the initial study reported by Russell (1974) in which hybrids for each
of the decades since 1930 were reconstructed from lines used during each decade. The hybrids were evaluated in replicated trials that emulated production practices used during the different decades (e.g., lower versus higher stand densities; lower versus higher nitrogen fertilizer rates; and hand versus machine harvesting). All hybrids from each decade were evaluated under the same experimental conditions, which permitted the separation of the genetic and environment effects. Yield was the trait of greatest interest, but data also were reported for other traits that are considered in breeding programs (Table 8-1).

Russell (1985) summarized information from 13 studies that estimated the portion of total gain in yield that can be attributed to genetic improvement of hybrids. The time span for each of the studies was from 1930 to the 1970s, and all except one were conducted in Iowa. Hybrids included in the studies, however, would be representative of those used in the central U.S. Corn Belt during the respective decades. The average total yield improvement from 1930 to 1980 was 0.927 q/ha/yr, of which 0.616 or 63.6% was attributed to genetic improvement.

The genetic gains in yield were made by developing hybrids that adapted to changes in management practices for maize production. Inbred lines and hybrids were developed that would respond to greater levels of nitrogen fertilizer, tolerate greater plant densities, and had greater levels of resistance to common pests. Russell (1984) reported that the average yield of 1930-era double-cross hybrids was 81.1 q/ha versus 83.9 q/ha for 1970-era single-cross hybrids evaluated at 31,000 plants per hectare, the stand density commonly used in the 1930s. Yields of the same hybrids evaluated at the stand density of 64,500 plants per hectare commonly used at present were 79.2 q/ha for the 1930-era hybrids versus 100.5 q/ha for the 1970-era hybrids. The 1970-era single-cross hybrids had the ability to respond to higher plant densities used in the 1970s, whereas the 1930-era double-cross hybrids were adapted to lower stand densities.

Genetic changes also have been made for other traits for the different era hybrids (Du Vick, 1984; Russell, 1984, 1985). Changes in the other traits were, in most instances, the result of correlated effects from selection for greater grain yield per se. Russell (1985) reported data for changes in 18 plant and ear traits for hybrids that were representative of six eras from 1930 to 1980. Differences among hybrids were significant for all traits, except ears per plant. The 1980-era hybrids were 18.7% greater yielding than 1930-era hybrids. The changes accompanying greater yield included earlier flowering, greater grain filling period from flowering to physiological maturity, greater kernel weight, greater shelling percentage, and better stay-green, an indication of overall plant health.

Genetic improvement also has been realized in maize populations, which are sources of germplasm for development of inbred lines and hybrids. Since the 1940s, several recurrent selection schemes have been
suggested and tested for improvement of maize cultivars. Objectives of these studies are to improve the gene frequency of the favorable alleles for the traits under selection and to maintain genetic variability for continued selection. Summaries of the recurrent selection methods and empirical data evaluating the effects of recurrent selection were made by Sprague and Eberhart (1977) and Hallauer and Miranda (1981). In all instances, selection was effective for the trait under selection. Grain yield received greatest attention, and rate of gain was about 2 to 4% per cycle for all methods of selection. Improvement of maize germplasm should provide sources of breeding materials for continued genetic gains in future hybrids.

Inheritance of Principal Traits

The genetic control of traits commonly included in breeding programs ranges from single major genes to complex inheritance. The maize genome is well mapped, but maize breeders usually do not emphasize selection for qualitative characters. Several traits have been studied during the past 50 years that modified either the kernel composition (sugary, waxy, opaque, and floury) or plant morphology (brachytic, liguleless, brown midrib, and tassel seed). In most instances, these traits were conditioned by single major alleles whose expression was not affected by the environment. The traits have contributed little, if any, to the genetic gains expressed in lines and hybrids. There are, however, a few major genes that have been used to correct a specific weakness in otherwise desirable lines and hybrids. The discovery by Hooker (1961) of the \( H_t \) gene for conditioning resistance to the fungus \( Helminthosporium turcicum \) has provided a useful gene for increasing the level of resistance to leaf damage. The gene can be incorporated into inbred lines by backcrossing.

Most traits considered of economic importance to maize breeders are quantitatively inherited. They are conditioned by a large, unknown number of loci. It generally is not possible to classify individuals into discrete classes based on their phenotypes because each locus has only a small effect on the expression of the trait. Additionally, the expression of the loci is affected by environment effects. Variability among individuals and progenies for quantitatively-inherited traits approximates a normal density distribution. Statistical parameters are used to determine the heritability of quantitative traits. Data are recorded on phenotypes (\( P \)), and the variability among phenotypes is partitioned to determine the relative importance of genetic (\( G \)) and environmental (\( E \)) effects. If an additive linear model of independent variables is used to describe the phenotype (\( P = G + E \)), the phenotypic variability is \( \sigma_P^2 = \sigma_G^2 + \sigma_E^2 \). If there
is no interaction of genotypes with environments ($\sigma_{p_e}^2$) the phenotypic variability is $\sigma_p^2 = \sigma_h^2 + \sigma_e^2$.

Heritability estimates of quantitative traits depend on the type of progenies evaluated and the environments sampled. It is necessary to define precisely the estimates of heritability (Hanson, 1963). In maize, there can be as much variation among estimates of heritability for the same trait as among estimates for different traits. Heritability ($h^2$) is calculated as $\frac{\sigma_h^2}{\sigma_p^2}$. Based on the expectations, an estimate of $h^2$ can be calculated as

$$\frac{\sigma_h^2}{\frac{\sigma^2}{r} + \frac{\sigma_{pe}^2}{e} + \sigma_e^2}$$

The estimate of $h^2$ depends on the types of progenies (half-sib, full-sib, $S_1$, $S_2$, etc.) evaluated, experimental error ($\sigma^2$), and the number of replications ($r$) used in the sample of environments ($e$). For example, if half-sib families are evaluated in two replications at three environments, the estimate of $h^2$ for yield may be 45%. If, however, $S_2$ progenies are evaluated in two replications at three environments, the estimate of $h^2$ for yield may be 80% or greater. In both instances, the estimates of $h^2$ may be greater if additional replications and environments are included. On an individual plant basis, $h^2$ may be less than 10%. Hence, heritability estimates of quantitative traits are specific to the population and to the environments sampled.

Hallauer and Miranda (1981) summarized estimates of $h^2$ for different ear and plant traits (Table 8-2). The estimates of $h^2$ are averages of reported studies and are given on a plot basis ($e = r = 1$). The estimates of $h^2$ were converted to a common basis to reduce the effects of $r$ and $e$ on the relative magnitude of the estimates. Grain yield and components of yield (ear and kernel traits) tend to have lower $h^2$ estimates, plant structural traits intermediate estimates, and traits related to maturity the highest estimates. The estimate of $h^2$ for oil percentage of the grain was 77%, which suggests the genetic variance relative to the phenotypic variance among plots for oil percentage is considerably greater than for yield.

Estimates of $h^2$ depend on having an effective screen to separate the genetic and environmental effects. For diseases and insects, the separation of these effects is enhanced by use of artificial means of infestation and infection and use of additional replications and environments. The estimate of $h^2$ for stalk lodging was zero because conditions did not exist to determine genetic differences among progenies for stalk strength (Table 8-2). If favorable environmental conditions exist, such as infection by stalk rot inciting fungi accompanied by strong winds, the genetic dif-
Table 8-2  Average Estimates of Heritability

(h²) for 17 Traits of Maize on a Plot Basis

<table>
<thead>
<tr>
<th>Traits</th>
<th>Number of Estimates</th>
<th>h²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grain yield</td>
<td>99</td>
<td>19%</td>
</tr>
<tr>
<td>Ear length</td>
<td>36</td>
<td>38</td>
</tr>
<tr>
<td>Ear diameter</td>
<td>35</td>
<td>36</td>
</tr>
<tr>
<td>Number of ears</td>
<td>39</td>
<td>39</td>
</tr>
<tr>
<td>Kernel Row number</td>
<td>18</td>
<td>57</td>
</tr>
<tr>
<td>Kernel weight</td>
<td>11</td>
<td>42</td>
</tr>
<tr>
<td>Kernel depth</td>
<td>7</td>
<td>29</td>
</tr>
<tr>
<td>Cob diameter</td>
<td>6</td>
<td>37</td>
</tr>
<tr>
<td>Grain moisture</td>
<td>4</td>
<td>62</td>
</tr>
<tr>
<td>Days to flower</td>
<td>48</td>
<td>58</td>
</tr>
<tr>
<td>Plant height</td>
<td>45</td>
<td>57</td>
</tr>
<tr>
<td>Ear height</td>
<td>52</td>
<td>66</td>
</tr>
<tr>
<td>Stalk lodging</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Number of tillers</td>
<td>5</td>
<td>72</td>
</tr>
<tr>
<td>Husk extension</td>
<td>3</td>
<td>50</td>
</tr>
<tr>
<td>Husk score</td>
<td>3</td>
<td>36</td>
</tr>
<tr>
<td>Percentage oil</td>
<td>4</td>
<td>77</td>
</tr>
</tbody>
</table>

Adapted from Hallauer and Miranda. 1981.

Differences can be detected and h² for stalk lodging may be 40 to 60%. Breeders have developed effective screens for several pests of maize, which increase h² and, therefore, increase effectiveness of selection. Heritability for resistance to first-generation leaf feeding by the European corn borer can range from 0 to 60%. If selection relies on natural infestation, h²’s may be zero because the pest either was not present or leaf feeding damage very erratic among progenies. Heritability can be increased if all progenies are uniformly infested with larvae.

**STEPS IN CULTIVAR DEVELOPMENT**

Cultivars of maize can be of several types. They can range from highly heterozygous and heterogeneous open-pollinated cultivars to homozygous and homogeneous inbred lines used to produce heterozygous and homogeneous single-cross hybrids. The type of cultivar grown in a particular area of the world depends on the economic development and infrastructure necessary to produce and distribute the seed. Within the United States and other advanced production areas, essentially 100% of the maize grown is hybrids. Within many areas of the lesser developed countries, open-pollinated cultivars or improved synthetic cultivars are commonly used. The more common situation in many areas of the world is a
combination of the two extremes: hybrids are used by the larger progressive farmers who have the necessary capital to purchase seed and other inputs for intensive maize production, whereas open-pollinated and improved synthetic cultivars are used by the subsistent farmers. Use of hybrid cultivars, however, is spreading rapidly throughout the world. It seems that, by the end of the twentieth century, use of open-pollinated cultivars will be restricted to local areas that are either extremely poor agronomically or geographically remote. Hence, methods considered for cultivar development in the remainder of the chapter will be restricted to development of inbred lines and hybrids.

The length of time needed to develop a hybrid is usually 10 to 15 years. Duvick (1977) calculated the average time frame at 13.3 years. Time required to develop new lines and hybrids varies among breeding programs because of seasons available for breeding activities, source material used for extraction of lines, extent of testing, and resources available to increase lines and produce hybrids for distribution to the farmers. Efficient use of off-seasons nurseries can be used to reduce the length of time for line development, but in most instances off-season nurseries may not be either desirable or amenable for effective selection, production of adequate seed for testing, and evaluation of lines in crosses. With efficient use of growing seasons, the cycle time for development of new hybrids by the pedigree method of breeding may be only 4 to 6 years.

There are five basic phases in hybrid development. Decisions have to be made for each phase, which are crucial in the ultimate success of the program. The five phases and the decisions that have to be made for each are: (a) choice of germplasm to initiate selection; (b) choice of selection methods used in the extraction of lines; (c) choice of testers to obtain initial estimates of combining ability; (d) choice of lines to cross and extent of testing; and (e) final choice of hybrid for production and distribution. Although extensive basic research has been reported for most phases, the decisions often involve judgment based on practical experience because of differences in objectives, breeding materials, and research capabilities among breeding programs. These differences affect the strategies used in each phase and either shorten or lengthen the time required for cultivar development. The sequence of activities in hybrid development are outlined in Table 8-3.

Because the sources of germplasm available to maize breeders are extensive, it is essential that a thorough study be made of available germplasm that will contribute to the breeding objectives. If the germplasm source has a very low frequency of favorable alleles for the important traits considered in developing new lines and hybrids, selection may be either futile or have very low probability of success. It is necessary to review the literature, study reports of yield test trials, and visit with colleagues in making intelligent choices of germplasm. After one has had ex-
<table>
<thead>
<tr>
<th>Year</th>
<th>Season</th>
<th>Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Winter</td>
<td>Self S₀ plants to obtain S₁ seed for 500* selected plants. Self S₁ plants within desirable S₀.₁ lines and select 180 plants to advance to the S₂ generation.</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Winter</td>
<td>Self S₀ plants within desirable S₁₂₂ lines and select 80 plants to advance to the S₃ generation.</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>Self S₀ plants within desirable S₂₂₂ lines and select 40 plants to advance to the S₄ generation.</td>
</tr>
<tr>
<td>3</td>
<td>Winter</td>
<td>a. Self selected S₁ plants within desirable S₃₄₄ lines to advance to the S₅ generation. b. Cross S₃₄₄ lines to appropriate tester (s)†.</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>a. self S₂ plants within desirable S₄₅₅ lines to advance to the S₆ generation (bulk plants if line is uniform). b. Evaluate the testcrosses of S₅₅₅ lines in replicated trials.</td>
</tr>
<tr>
<td>4</td>
<td>Winter</td>
<td>a. Self S₂ plants within desirable S₄₅₅ lines to advance to the S₆ generation. b. Make testcrosses of selected S₅₅₅ lines.</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>a. Grow S₅₅₅ lines and make final selections b. Bulk uniform lines and increase for breeder seed. c. Produce seed of single-cross hybrids.</td>
</tr>
<tr>
<td>5</td>
<td>Summer</td>
<td>a. Grow S₇₅ lines and increase to provide breeder seed. b. Evaluate single crosses in replicated trials.</td>
</tr>
<tr>
<td>6†</td>
<td>Summer</td>
<td>a. Seed increase of elite inbred lines. b. Produce single crosses for further evaluation. c. Evaluate single crosses in replicated trials produced the previous year.</td>
</tr>
<tr>
<td>7‡</td>
<td>Summer</td>
<td>a. Produce larger quantities of seed of elite inbred lines either by hand pollination or in isolation. b. Produce seed of single crosses for more extensive testing. c. Evaluate single crosses produced the previous year.</td>
</tr>
<tr>
<td>8‡</td>
<td>Summer</td>
<td>a. Evaluate elite inbred lines for purity. b. Determine the production potential of the inbreds as male and female parents. c. Produce sufficient seed of the inbreds for possible use in commercial hybrids. d. Conduct strip tests and additional replicated trials of single crosses with potential as commercial hybrids.</td>
</tr>
<tr>
<td>9</td>
<td>Summer</td>
<td>a. Conduct strip tests to determine farmer acceptance. b. Begin small-scale commercial production of elite hybrids.</td>
</tr>
<tr>
<td>10</td>
<td>Summer</td>
<td>If hybrid performance and farmer acceptance meet the standards required for commercial production, a final decision is made to produce the hybrid for sale.</td>
</tr>
</tbody>
</table>

*Number of progenies selected each generation based on a survey conducted by Bauman (1981).
†Based on a survey by Bauman (1981), 18% of maize breeders would conduct the first testcross trials with S₁₂₂ lines, 33% with S₁₃₂ lines, and 27% with S₂₄ lines.
‡Activity would be optional in winter season and may not be considered appropriate at this stage.
§Activity could be completed in years 4 and 5, which would shorten the time 2 to 3 years (Troyer, 1978).
perience in developing lines and hybrids, the choices of germplasm are easier.

Choice of breeding and selection methods is limited only by the imagination of the breeder. In some instances, the selection method may be dictated by the objectives of selection, whereas in others it may be dictated by policy. In most instances, however, the selection methods are a personal preference based on training, interests, and experience. The emphasis in selection will vary among individuals and traits based on relative importance placed on the art versus science of plant breeders. Breeders who emphasize the art of breeding feel that they can effectively visually select for certain traits. Those who emphasize science feel that replicated trials are needed. Emphasis given to visual selection varies among traits (Table 8-1). Inbreeding is emphasized during selection to derive new inbred lines. Inbreeding can be accomplished by different methods of mating, but self-pollination is usually preferred.

The ultimate use of new inbred lines is as parents in the production of hybrids. It is essential, therefore, to determine if the lines transmit their desirable traits in hybrids. At some stage during inbreeding and selection, two decisions have to be made: (a) the stage of inbreeding at which to obtain a measure of combining ability of new lines, and (b) the tester to use in evaluating combining ability. There are proponents for testing in early generations of inbreeding (S₅ to S₇) and others who prefer testing in later generations (S₈ or later). Bauman (1981) reported that 60% of maize breeders preferred a compromise between early and late generation testing. None advocated test crosses at the S₅ and S₆ generations, and only 13% preferred to test at some generation beyond the S₈ generation. Those who prefer later testing feel they can visually discard progenies during inbreeding and selection and test only those lines that are acceptable for practical use in commercial production of hybrids.

An important decision in hybrid development is the choice of testers used to evaluate new lines. The choice of tester is obvious in some instances, and not in others. If an obvious heterotic pattern has been established (e.g., 'Reid Yellow Dent' versus 'Lancaster Surecrop' in the U.S. Corn Belt), the tester is chosen that represents the opposite side of heterotic pattern from the inbred under consideration. If lines are developed from sources that include germplasm from both sides of heterotic pattern or from unrelated sources, the choice of tester may not be as obvious. Tester choice also may be dictated by a line that is widely used in seed production.

The success of the time and effort expended in choosing germplasm to initiate selection, breeding, and testing methods is judged by the performance of the new hybrids derived from the program. The results may be either very rewarding or extremely frustrating. Lines that survive selection during inbreeding and have good testcross performance are mated to
produce single-cross hybrids. Replicated trials of new single crosses are conducted over locations and years to determine their relative performance compared with the hybrids currently in production. If any new hybrids are judged superior to current hybrids, trials are expanded over greater areas. After superior lines have been identified in public programs, they are released for use by private breeders. The private breeders will evaluate the usefulness of the lines in new hybrid combinations. If a new hybrid is judged to be superior to those currently on the market, the private company will increase seed of the parent lines for production of the hybrid on a large scale. The success of the breeding program is measured by the final product: a new superior hybrid that is accepted over a large area and provides an economic return on the investment in research and development.

SOURCES OF GENETIC VARIABILITY

Origin of Cultivated Species

Maize is one of the few major crop species of the United States that is indigenous to the Western Hemisphere. It was an important component of the Indian civilizations when the European colonists arrived in the Western Hemisphere. The transformation of maize from a wild, weedy species to a domesticate probably occurred 7000 to 10,000 years ago. By the time the European colonists arrived, most of the nearly 250 to 300 races of maize were developed. Primitive maize breeding methods were effective in developing races and cultivars to satisfy their cultural requirements based on easily recognizable phenotypes (kernel color and type) and environmental conditions (maturity, altitude, drought, pests). Early maize breeders developed a wealth of germplasm that has contributed to the productivity and stability of modern maize hybrids.

Maize is a member of the grass family in the tribe Maydeae (Table 8-4). The tribe Maydeae includes seven genera, two of which are native to the Western Hemisphere (Zea and Tripsacum) and five that are native to Asia. The genus Zea includes four species commonly called teosinte (Z. mexicana, Z. perennis, Z. luxurians, and Z. diploperennis) and maize (Z. mays). The teosinte species are weedy in appearance, but in most instances can be crossed readily with maize. The genus Tripsacum is widely dispersed in the Western Hemisphere and includes several perennial species with different ploidy levels (Brink and de Wet, 1983). The resemblance between maize and Tripsacum is much less than between maize and teosinte. Whereas maize and teosinte are crossed relatively easily, special techniques are required to cross maize and Tripsacum. The somatic chromosome number of maize is 2n = 20, which is the same as that of
Table 8-4  Genera and Species Included in the Tribe *Maydeae*

<table>
<thead>
<tr>
<th>Western Hemisphere</th>
<th>Asia</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Genera</strong></td>
<td><strong>Genera</strong></td>
</tr>
<tr>
<td><strong>Species</strong>*</td>
<td><strong>2n</strong></td>
</tr>
<tr>
<td>Zea mays</td>
<td>20</td>
</tr>
<tr>
<td>Z. diploperennis</td>
<td>20</td>
</tr>
<tr>
<td>Z. luxurians</td>
<td>20</td>
</tr>
<tr>
<td>Z. mexicana</td>
<td>20</td>
</tr>
<tr>
<td>Z. perennis</td>
<td>40</td>
</tr>
<tr>
<td>Tripsacum andersomii</td>
<td>64</td>
</tr>
<tr>
<td>T. austral</td>
<td>36</td>
</tr>
<tr>
<td>T. bravum</td>
<td>36,72</td>
</tr>
<tr>
<td>T. cundinámbarce</td>
<td>36</td>
</tr>
<tr>
<td>T. dactyloides</td>
<td>36,72</td>
</tr>
<tr>
<td>T. florianum</td>
<td>36</td>
</tr>
<tr>
<td>T. intermedi</td>
<td>72</td>
</tr>
<tr>
<td>T. manisuroides</td>
<td>72</td>
</tr>
<tr>
<td>T. latifolium</td>
<td>36</td>
</tr>
<tr>
<td>T. peruvianum</td>
<td>72,92,108</td>
</tr>
<tr>
<td>T. zopilotense</td>
<td>36,72</td>
</tr>
<tr>
<td>T. jalapense</td>
<td>72</td>
</tr>
<tr>
<td>T. lanceolatum</td>
<td>72</td>
</tr>
<tr>
<td>T. laxum</td>
<td>36</td>
</tr>
<tr>
<td>T. maiz</td>
<td>36,72</td>
</tr>
<tr>
<td>T. pilosum</td>
<td>72</td>
</tr>
</tbody>
</table>

*Species for the two sections (*Tripsacum* and *Fasciculata*) of *Tripsacum* were provided by J. M. J. de Wet (personal communication, 1985).

Z. mexicana, Z. luxurians, and Z. diploperennis. Z. perennis, a perennial species thought to be derived from Z. mexicana, is a tetraploid (2n = 40) form of teosinte. *Tripsacum* species have somatic chromosome numbers that are usually multiples of 18.

Four hypotheses have been advanced as to the possible origin of maize. (a) Weatherwax (1955) proposed that maize, teosinte, and *Tripzacum* descended from a common, extinct ancestor native to the highlands of Mexico or Guatemala. (b) Anderson (1945) suggested that maize originated from a cross between two species, perhaps *Coix* and *Sorghum*, each with 10 chromosomes. (c) Mangeldorf and Reeves (1939) developed the tripartite hypothesis that suggested wild maize was a form of pod corn native to lowlands of South America, teosinte originated from crossing cultivated maize and *Tripsacum* in Central America, and modern cultivars of maize arose from crosses between wild maize (pod corn) and
*Tripsacum* or teosinte. (d) Beadle (1939), and others, have suggested that maize was derived from teosinte by direct selection. Although the ancestry of maize has been extensively studied, its exact origin has not been resolved. Some portions of the hypotheses for the origin of maize have been modified as additional information became available (Galinat, 1977). Except for Anderson (1945), none of the Asian genera has been considered in the origin of modern maize.

**Types of Parents and Populations**

Maize breeders usually have an adequate reservoir of genetic variability to realize progress from selection. Genetic variability available to maize breeders is of two types: (a) naturally occurring genetic variability within broad-based populations including races, accessions, landrace cultivars, and improved synthetic cultivars, and (b) genetic variability generated by crossing inbred lines and either self-pollinating or random mating the segregating progeny.

In the early years of hybrid development, the adapted landrace cultivars were the primary types of populations used. They were usually genetically variable because of natural outcrossing within themselves and with other cultivars. Inbreeding and selection were initiated by sampling desirable plants within the landrace cultivars and eventually identifying elite lines to produce double-cross hybrids. The first inbred parents of commercial hybrids had deficiencies that limited their use. The landrace cultivars often were resampled to develop better lines, but the procedure generally was not effective. If an otherwise desirable inbred parent was deficient for one trait that was present in another line, backcrossing techniques were used to improve the inbred.

Source populations preferred by current maize breeders were summarized by Bauman (1981), and the relative importance of source populations anticipated in the future was reported by Hallauer (1979) (Table 8-5). Maize breeders presently prefer genetically narrow-based populations, including elite-line synthetics with a restricted genetic base, F₂ populations of single crosses, and backcross populations. It is anticipated that these same types of populations will receive the same or greater emphasis in the future. The original open-pollinated landrace cultivars and double-cross hybrid populations will be of lesser importance in the future as sources of inbred lines.

The trend in types of populations used in breeding programs was noted by Jenkins (1978). Since 1936, pedigree selection in single-cross and backcross populations has increased dramatically. Zuber and Darrah (1980) listed the 40 most widely used public lines for producing commercial hybrids. Thirty-four of the lines were derived from pedigree selection
Table 8-5  Types of Populations preferred by Maize Breeders and Effort Devoted to Each Source

<table>
<thead>
<tr>
<th>Population Source</th>
<th>Rating of Sources*</th>
<th>Percent of Total Effort</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bauman (1981)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Genetically broad-based</td>
<td>2.6</td>
<td>15</td>
</tr>
<tr>
<td>Genetically narrow-based</td>
<td>2.0</td>
<td>16</td>
</tr>
<tr>
<td>Elite-line synthetic†</td>
<td>1.8</td>
<td>14</td>
</tr>
<tr>
<td>Double-cross</td>
<td>3.1</td>
<td>2</td>
</tr>
<tr>
<td>Single-cross</td>
<td>1.9</td>
<td>22</td>
</tr>
<tr>
<td>Related-line cross</td>
<td>2.0</td>
<td>15</td>
</tr>
<tr>
<td>One backcross</td>
<td>1.9</td>
<td>12</td>
</tr>
<tr>
<td>Two backcrosses</td>
<td>2.6</td>
<td>5</td>
</tr>
</tbody>
</table>

Percent Emphasis Given in Future

<table>
<thead>
<tr>
<th></th>
<th>More</th>
<th>Same</th>
<th>Less</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hallauer (1979)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open-pollinated cultivars</td>
<td>3</td>
<td>6</td>
<td>91</td>
</tr>
<tr>
<td>Synthetic cultivars</td>
<td>42</td>
<td>55</td>
<td>3</td>
</tr>
<tr>
<td>Exotic germplasm</td>
<td>42</td>
<td>45</td>
<td>13</td>
</tr>
<tr>
<td>Single-cross</td>
<td>26</td>
<td>55</td>
<td>19</td>
</tr>
<tr>
<td>Backcross</td>
<td>16</td>
<td>61</td>
<td>23</td>
</tr>
<tr>
<td>Others†</td>
<td>59</td>
<td>41</td>
<td>0</td>
</tr>
</tbody>
</table>

* Ratings are 1 to 4, where 1 was of greatest importance and 4 was of least importance.
†Genetically narrow-based synthetic cultivars are formed with a number of related or unrelated elite lines.
††Primarily synthetic cultivars improved by selection and may be either genetically broad- or narrow-based.

in single-cross or backcross populations. Five lines (B14, B37, B73, B84, and N28) were derived from Iowa Stiff Stalk Synthetic and one (K55) from 'Pride of Saline,' an open-pollinated cultivar. It is clear that the open-pollinated landrace cultivars used as source populations before 1936 are of minor importance in modern breeding programs.

At least 85% of the maize breeding effort involves the use of elite inbred lines as parents of breeding populations (Table 8-5). Pedigree selection is emphasized within populations with a restricted genetic base, whether they are synthetic cultivars or single-cross and backcross populations. Hallauer and Miranda (1981) estimated that more than 1 million lines have been evaluated in testcrosses. The number of elite lines, how-
ever, has been relatively limited, and they have been recycled in selection programs because they contribute traits that are desired by breeders. For example, B14 has been a popular inbred parent for the development of source populations due to its good stalk strength and rapid dry down. Breeders prefer to initiate inbreeding and selection in populations that have a greater probability of yielding lines that meet modern-day standards. The chances of obtaining superior new lines in a synthetic cultivar developed from lines related to B14, such as B14A, B64, B68, A632, A634, and A635, are greater than in ‘Reid Yellow Dent,’ an open-pollinated cultivar that was widely grown before the advent of hybrids.

The performance of the lines per se and in crosses are considered in choosing parents. Lines that transmit their traits to hybrids are preferred. The change in recent years from the use of double-cross hybrids to the use of single-cross hybrids has, however, placed greater emphasis on inbred line performance per se. Modern hybrids must have high yield, stable performance, adequate root and stalk strength to remain upright for mechanical harvesting, adequate pest resistance to reduce chances for economic losses, and early enough maturity to avoid frost injury. Very few, if any, lines and hybrids are satisfactory for all traits. Consequently, breeders choose the best lines available and attempt to correct the weakest trait of the respective lines.

In recent years, C103, B14, B37, B73, and Oh43 have been used extensively as one of the parents in single-cross or backcross populations. Mo17 was selected from the single cross of 187-2 × C103 and it has better ear expression than C103. A632, another widely used inbred, was derived from the backcross population of Mt42 × B14 and has earlier maturity than B14. In 1981, of the lines released from public breeding programs, 68 had germplasm from C103, 71 from B14, 27 from B37, 14 from B73, and 53 from Oh43. Parents of breeding programs, therefore, include lines that have proven performance and have contributed to producing successful hybrids. Lines are recycled to correct weaknesses and enhance performance and stability of their hybrids.

**Procedures for Artificial Hybridization and Self-Pollination**

Because maize is monoecious and naturally cross-pollinated, it is relatively easy to produce seed by artificial hybridization and self-pollination. The principal barrier to artificial hybridization is synchronization in the development of male and female flowers of the parents being hybridized. This usually can be accomplished by staggered planting dates for the parents. If one parent flowers 10 days earlier than the other, the earlier flowering parent can be delayed in planting. Experience and familiarity with the materials usually help in determining the appropriate planting dates. If
staggered plantings are not used, flowering also can be either delayed or enhanced by use of fertilizer, clipping, and flaming treatments (Russell and Hallauer, 1980).

Cross- or self-pollination produce adequate seed from an individual plant for most breeding purposes, if proper procedures and precautions are used. Although it is relatively easy to hybridize and self-pollinate in maize, it is necessary to use proper methods to maintain the parentage of the seed produced. It is necessary to cover the tassels and ear shoots to prevent contamination by pollen being circulated in the field by wind currents.

Equipment and supplies needed to produce seed by controlled pollinations are easily obtained (Fig. 8-3). The equipment includes a heavy-duty carpenter's apron with pockets designed to include materials to cover the tassels (tassel bags) and ear shoots (shoot bags); paper clips or stapler; a paring knife of convenient size to prepare the ear shoots; and a soft-leaded marking pencil for making notes on either the tassel or shoot bags [Fig. 3(a)]. There are different sizes, types, and quality of equipment and materials, and the items used depend on personal preference and cost. Some breeders prefer the use of a stapler to attach bags to the tassel and ear shoot, while others prefer the use of brass-coated paper clips. Some prefer use of a grease pencil rather than use of a soft-leaded carpenters pencil for marking the tassel and shoot bags. The tassel and shoot bags are available in different weights and sizes. It is important that all tassel and shoot bags be water repellant and made with moisture-proof glue.

Artificial pollination, whether crossing or selfing, requires a series of procedures that must be followed to produce good quality, contamination-free seed. The plants within each progeny must be checked daily at flowering to cover the ear shoots. Ear shoots must be covered before silks have emerged from the tip of an ear shoot to avoid fertilization by pollen of unknown origin. Shoot bags are placed over each ear shoot and firmly anchored between the ear shoot and auricle of the ear leaf to prevent removal by wind currents [Fig. 3(b)]. The covering of ear shoots should be one of the first tasks done each morning to prevent loss of ear shoots due to silk emergence. Frequent and conscientious checking of plants to cover ear shoots is the most critical phase of artificial pollination.

Ear shoots that have full silk emergence 2 to 3 days after they have been covered are the most desirable for use in making pollinations. Ear shoots are checked daily, and when they are at the proper stage, tassels are examined to determine if viable pollen is available to fertilize the female gametes. Tassels used to pollinate the ear shoot either may be on the same plant as the ear shoot (self-pollination) or another plant (cross-pollination). When the tassels and silks are at the proper maturity for pollination, both have to be prepared. Pollinations are made the day following the preparation of the male and female flowers. The females are
Figure 8-3  Equipment and techniques used in artificial pollination of maize. (A) equipment required for hand pollination; (B) bag placed over ear shoot before silk emergence; (C) ear shoot being prepared for pollination; (D) ear shoot ready for pollination; (E) tassel bag secured to tassel; (F) pollen from tassel applied to ear shoot; and (G) tassel bag secured to plant of pollinated ear shoot.
prepared by cutting the tip of the ear shoot within 2 cm of the husk tip [Fig. 3(c)]. This procedure causes the formation of a brush of silks on which the pollen can be applied the following day [Fig. 3(d)]. Cutting off the tip of ear shoot also ensures a brush of silks that is representative of the ear. The cutting of silks usually results in better seed set and less contamination. Silks usually cannot be cut more than once because regrowth after the second cut is poor or does not occur. The shoot bag must be replaced securely after preparation of the ear shoot.

After the ear shoot has been prepared, the appropriate tassel must be prepared as a source of pollen. If the prepared ear shoot is to be self-pollinated, the tassel of the same plant is prepared immediately after the ear shoot is prepared. For cross-pollinations, tassels are prepared on different plants. Viable pollen can be obtained from an uncovered tassel the same day ear shoot is prepared, but possible contamination may occur
from foreign pollen that may adhere to the tassel. The tassels usually produce their greatest volume of pollen 2 or 3 days after the start of pollen dehiscence, and this period is usually coincident with the time of optimum silk emergence. Tassel bags are placed over the tassels of the intended source of pollen and securely fastened to the peduncle to withstand loss by wind and rain [Fig. 3(e)]. Tassel bags may be secured by paper clips or staplers, but paper clips usually are preferred for ease in removal of tassels at time of pollination.

Pollination is accomplished approximately 24 hours after the tassels and ear shoots have been prepared. Pollination must wait until anthers have exerted and pollen is released. This occurs about 3 hours after sunrise, but it may occur earlier or later depending on the temperature and humidity. Pollen bags must be dry to prevent clumping of pollen, which may not be viable. If the day continues wet and humid because of rain, pollination may be delayed until the following day. Pollen dehiscence under the bag will not be complete without shaking or tapping the tassel bag before it is removed from the plant. After the tassel bag has been shaken, the tassel is tilted and the tassel bag containing the viable pollen is carefully removed. Care should be taken not to expose the inside of bag to possible contamination with other pollen in the field. The contents of the tassel bag are poured on the brush of silks on the ear shoot [Fig. 3(f)]. The silks may be exposed by either tearing of the end of the shoot bag or carefully lifting up the shoot bag to expose the silks. Each operation should be conducted as quickly as possible to minimize chances of contamination. After pollen has been applied, the tassel bag is placed over the ear shoot and fastened to the culm. Bags should be securely fastened by paper clips or staples [Fig. 3(g)]. The tassel bag will remain over the ear shoot until harvest.

One can usually expect good success with hand pollination in maize. The main constraints are adverse environmental factors (drought, heat, rain) that affect flower development and pollination. With a minimum of training and experience, individuals can become adept at making successful pollinations with good seed set (Russell and Hallauer, 1980).

**Mutagenesis**

Except for some specific loci used in genetic studies, mutable agents have not been used in maize. An extensive selection study was conducted by Gardner (1977), which compared the effects of mass selection in two subpopulations of 'Hays Golden,' an open-pollinated cultivar. Mass selection was conducted in one subpopulation representative of the original cultivar and in another subpopulation where the seed of the original population and a population formed after two cycles of selection received thermal
neutron irradiation. After 18 cycles of mass selection, response to selection was measured in both subpopulations. Rates of response of 3% per cycle for the first 16 cycles were similar for both subpopulations, with no indication that useful genetic variability was greater in the irradiated subpopulation. The results obtained by Gardner (1977) suggested that genetic variability was not limiting in the original population.

Mutation breeding in the conventional context has not been an important component of maize breeding programs. Recent evidence of genetic variability among progenies generated via tissue culture may change breeding strategies in the future. Although it is not clear how the variation arises via tissue culture, somoclonal variation may play a greater role in the future, particularly for alleles at specific loci for maturity, pest resistance, herbicide tolerance, and salt tolerance. Induced mutations, in this context, may permit modification of elite lines for specific traits.

**BREEDING PROCEDURES**

Maize breeding can be partitioned into three major time sequences for the more commonly used methods: (a) 7000 to 10,000 years ago—conversion from a weedy species to a cultivated species; (b) to 1920—mass selection among and within the cultivated species to produce distinctive races and cultivars for specific environmental niches and cultural needs; and (c) 1909 to the present—development of the inbred-hybrid concept and identification of breeding and selection methods currently used to produce high performance single-cross hybrids.

Maize has been studied extensively, but conflicting views still exist as to its origin (Galatin, 1977). Although the recorded history for the origin of cultivated maize and the selection methods used to develop the more than 250 to 300 races of the species are not complete, the changes and advances before 1900 were greater than those that have yet occurred in the twentieth century (Russell, 1974). Mendelian genetics were not understood and experimental techniques were not available to the early maize breeders. But they were effective in developing the germplasm that has been the foundation of modern maize breeding programs. If the maize collections available in national and international germplasm banks are maintained in a viable condition, a wealth of genetic variation remains to be exploited.

Breeding methods and strategies developed during the twentieth century for maize improvement have changed rapidly. Three factors were instrumental in the development of maize breeding methods: rediscovery of Mendelian genetics; development of experimental designs, analyses of variance, and plot techniques; and the pure-line method of breeding suggested by Shull (1909). Maize breeding became more of a science than
an art during the twentieth century. Previous methods of maize breeding, such as mass selection, ear-to-row selection, and cultivar crosses, were rapidly replaced or ignored, and the inbred-hybrid concepts were emphasized. Tremendous effort and resources were committed to developing and testing Shull's concept. The results were positive, and it has been suggested that the breeding methods used to develop highly productive U.S. Corn Belt hybrids are one of the greatest achievements of plant breeding.

The maize breeding methods developed and used since 1909 have been described in detail (Sprague, 1946; Crabb, 1947; Hayes, 1963; Sprague and Eberhart, 1977; Hallauer and Miranda, 1981). Major developments included techniques for inbred line development, testing of inbred lines in hybrids, and genetic improvement of germplasm sources. Both theoretical and empirical studies were conducted, primarily by the publicly supported breeding programs. After the applied and technical aspects of developing and producing hybrids were resolved, many of the concepts were adopted by private programs. There was a free interchange of ideas and materials among public and private breeding programs until about 1970. The trend for the interchange of breeding materials is decreasing because of the passage of the Plant Variety Protection Act and the competitiveness of the commercial seed industry. Proprietary inbred lines and hybrids are closely guarded by the respective firms and are not made available. This may seem to reduce progress, but the rapid expansion of private breeding programs ensures a larger reservoir of inbred lines and hybrids within the total private sector.

Many breeding strategies have been suggested for developing new lines, modifying existing lines, and improving germplasm sources for extraction of new lines (Table 8-6). Pedigree selection is the most widely used method. Shull (1909) used the pedigree method to extract lines from an open-pollinated cultivar. Recently, it seems that pedigree selection generally is associated with extraction of lines from F2 populations developed from the single crosses of two inbred lines. But pedigree selection methods also are used in backcrossing programs and for the extraction of lines from populations improved by recurrent selection. Cumulatively, pedigree selection probably accounts for more than 95% of the breeding effort in maize. As the name pedigree implies, the method requires careful notes to maintain a record of parentage, generations of inbreeding, separation of sublines, and plant traits of each selection.

Two broad categories of breeding strategies are used in maize improvement: (a) development of either new or modified inbred lines, and (b) population improvement to provide improved sources of germplasm for development of new lines. The relative importance of the two categories has oscillated over time. Maize breeding before the twentieth century emphasized population improvement. With the advent of the con-
Table 8-6 Breeding Strategies that Emphasize Developing New Lines for Use in Hybrids and Improvement of Maize Populations

<table>
<thead>
<tr>
<th>Strategies</th>
<th>Method of Selection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Line development</td>
<td>Pedigree, Gamete sampling, Single-seed descent, Doubled monoploids, Androgenesis, Indeterminacy gametophyte, Pollen culture</td>
</tr>
<tr>
<td>Line modification</td>
<td>Backcrossing, Convergent improvement, Tissue culture</td>
</tr>
<tr>
<td>Population improvement</td>
<td>Mass, Ear-to-row, Half-sib, Full-sib, Inbred (S₁, S₂, etc.)</td>
</tr>
<tr>
<td>Intrapopulation</td>
<td>Half-sib</td>
</tr>
<tr>
<td>Interpopulation</td>
<td>Full-sib</td>
</tr>
</tbody>
</table>

cepts suggested by Shull (1909), population improvement was essentially ignored. From 1920 to 1950, attention was focused on developing lines for use in hybrids using the populations available, mostly the open-pollinated landrace cultivars. It was not until the 1940s and 1950s that interest in population improvement was revived.

Since the 1950s, greater emphasis has been given to population improvement, but it still is probably less than 5% of the total maize breeding effort in the United States. Several public programs emphasize population improvement with little attention given to development of new inbred lines, whereas most private programs emphasize inbred line and hybrid development. This partition of emphasis between breeding strategies will probably continue.

Three breeding strategies will be described in detail to illustrate the sequence of activities in hybrid development, one for each of the categories listed in Table 8-6. Pedigree selection and backcrossing are obvious choices for line development, but the choices among methods of population improvement are not as clear. Several options for population improvement are available and, at this time, they seem to be about equally effective (Hallauer and Miranda, 1981). The choice of a method, therefore, depends on the breeding objectives, how a method complements the applied breeding program, and whether one or two populations
are included. The breeding sequence for developing progenies, evaluating progenies in replicated trials, and recombining superior progenies to form the next population generally is the same for all methods of population improvement.

**S₂ Recurrent Selection**

Population improvement by recurrent selection among \( S_{1,2} \) lines, commonly referred to as \( S₂ \) recurrent selection, has not been used as extensively as the other methods of the same category (Table 8-6). Because evidence suggests that the preponderance of genetic variance within maize populations is due to additive effects and that stable, high-yielding inbred lines are needed to produce single-cross hybrids at reasonable costs, \( S₂ \) recurrent selection is receiving greater attention. \( S₂ \) recurrent selection also can contribute directly to applied breeding programs. Multiple-trait selection can be practiced among and within \( S_{0,1} \) and \( S_{0,2} \) lines for traits related to performance per se and pest tolerance.

An outline description of \( S₂ \) recurrent selection is given in Table 8-7. The activities listed for each season can be modified, depending on the number of seasons available each year and the activities that can be conducted during each season. For temperate areas, activities in seasons 1, 4, and 6 would be conducted in off-season nurseries (Table 8-7). There would be greater emphasis on selection among and within \( S_{0,1} \) and \( S_{1,2} \) lines if they were grown in areas in which the population was adapted. This does not infer that no selection is effective in off-season nurseries.

Selection can be practiced for foliar leaf diseases (e.g., *H. turcicum*) and insect damage (e.g., *Heliothis zea*), but the population may be severely damaged by pests (e.g., *Sclerospora* spp.) that are not indigenous to the projected areas of use. With the use of off-season nurseries, one cycle of \( S₂ \) recurrent selection would be completed in 3 years.

Decisions critical to the success of \( S₂ \) recurrent selection are made for each phase. The decisions affect the relative response of the population to selection by an increase in the frequency of favorable alleles for traits of interest and the usefulness of lines extracted from the population in applied breeding programs. The decisions include:

**Phase 1:** Choice of a population in which to initiate selection. Sample size required to sample genetic variability in a population. Effectiveness of selection among \( S₀ \) plants. Traits to select within and among \( S_{0,1} \) lines.

**Phase 2:** Number of \( S_{1,4} \) lines to include in replicated trials. Extent of replicated trials for measuring differences among lines. Number of lines to select for recombination.
Table 8-7  Sequence of Activities Used for the Improvement of Maize Populations by Use of $S_2$ Recurrent Selection

<table>
<thead>
<tr>
<th>Season</th>
<th>Breeding Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Self 500 to 1000 selected $S_0$ plants in the population chosen for improvement. An adequate sample is necessary to represent the genetic variability of the population. Selection is minimal among $S_0$ plants because the heritability is low for most traits of interest and usually selection is done in an off-season nursery.</td>
</tr>
<tr>
<td>2</td>
<td>Plant seed of $S_{0.1}$ lines in nurseries for breeding and for evaluation of pest resistance. One replication is usually satisfactory for the initial screening. Use artificial methods of infestation and infection to reduce escapes and increase heritability. Selections can be made before flowering for some traits (first-generation European corn borer), but must be delayed until harvest for others (stalk rot). Self $S_1$ plants. At harvest, select desirable $S_1$ plants for yield testing the following years.</td>
</tr>
</tbody>
</table>
| 3      | (a) Conduct replicated yield trials of $S_{1.2}$ lines. Include two replications at as many locations (3 to 4) as seed supplies permit. Collect, analyze, and summarize data from replicated trials and make selections. Select 25 to 35 lines as parents for a new population for the next cycle of selection.  
(b) Lines in the yield test also can be included in breeding nursery for use in an applied breeding program. $S_3$ plants are self-pollinated within desirable lines to advance to the $S_3$ generation. |
| 4      | (a) Selected lines are recombined by the use of remnant $S_1$ or $S_2$ seed. The bulk-entry method of intermating can be used. Harvest all ears produced by artificial hybridization and take an equal quantity of seed from each to form a bulk of 500 to 1000 seeds. Make two bulks and keep one in reserve in cold storage in case the population is lost in season 5.  
(b) In the applied breeding program, self $S_3$ plants within desirable $S_{2.3}$ lines to advance to the $S_4$. |
| 5      | Recombine the population developed in season 4. $S_{2.4}$ lines can be included in breeding nursery for continued inbreeding and selection and in the topcross nursery to produce seed for evaluation of combining ability. |
| 6      | Initiate the next cycle of selection by selfing selected $S_0$ plants in the population obtained by recombination in season 5. |

**Phase 3: Methods to use for recombination.** Remnant seed ($S_1$ or $S_2$) to be used for recombination. Number of generations of recombination between cycles of selection. Extent and method of sampling during recombination.

Information often is not available to make objective decisions about the alternatives available for each phase. In some instances, the optimum choice may not be practiced because of constraints within the breeding program. A sample of 3000 individuals from a population may
be more desirable than 300, which seems to be a minimum, but facilities and time may not permit screening a sample of 3000.

An adequate number of parents must be recombined each cycle to maintain genetic variability for future selection. Long-term selection programs require a larger number of parents than short-term selection programs. With short-term selection, 10 to 20 parents may be adequate, whereas 25 to 30 parents may be a compromise between short-term and long-term selection response. A larger number of parents is more difficult to intercross than a fewer number of parents. A fewer number of parents, however, may reduce response to selection because of the effects of genetic drift and inbreeding. Compromises usually are made within the constraints of a breeding program, as discussed by Hallauer and Miranda (1981).

Several methods of recurrent selection are available and are being used. Although the choice of method may be somewhat arbitrary, comparisons of the relative progress expected with different methods can be determined from use of the following relation:

$$\Delta G = \frac{k c \sigma^2}{y \sigma_p},$$

where $G$ is expected gain; $k$ is standardized selection differential; $c$ is parental control of progenies used in recombination; $\sigma^2$ is additive genetic variance among progenies tested; $y$ is number of years required to complete a cycle of selection; and $\sigma_p$ is the phenotypic standard deviation among progenies tested. Expected gain for different combinations of variables can be computed to determine the most efficient combination of factors for maximizing genetic gain (Hallauer and Miranda, 1981). Expected genetic gain can be increased if factors in the numerator of the equation are increased with no changes in the denominator, or by reducing factors in the denominator with no changes in the numerator. If a long-term recurrent selection program is envisioned, it behooves one to consider all factors to make it as efficient as possible for development of elite material for an applied breeding program.

A specific example is the progress realized from recurrent selection programs conducted in Iowa Stiff Stalk Synthetic (BSSS), which is a maize population developed from recombination of 16 inbred lines with above-average stalk strength. Recurrent selection was initiated in BSSS in 1939, the results of which were summarized by Hallauer et al. (1983). Response to different selection methods was realized, and there was no evidence of a plateau effect in the rate of genetic gain. A significant feature of the program has been the lines derived from the selected populations, and their contributions to the hybrid seed industry of the United States. Individuals chosen as parents for recombination to form the population for the next cycle of selection have been included in the applied
breeding and testcross nurseries for further selection and evaluation. Based on the applied breeding and testing program, superior lines have been released for use by the hybrid seed industry. Four lines derived from the recurrent selection in BSSS have had extensive use in commercial seed production for the past three decades (Hallauer et al., 1983). Russell (1985) summarized data for the four lines crossed to Mo17, a common tester. Data were obtained for 33 environments for 9 years (Table 8-8). B84 was extracted from the seventh cycle of selection and released in 1978. In comparison with B14, which was extracted from the original unselected BSSS population, B84 × Mo17 was 32.2% higher in yield than B14 × Mo17. It seems that the use of recurrent selection can contribute to continued genetic gains in hybrid yields.

Pedigree Selection

Pedigree selection is the most frequently used method for maize breeding and has been very effective in the genetic improvement of hybrid maize. The context within which pedigree is used has changed during the past 60 years. Shull (1909) initiated pedigree selection in an open-pollinated white-dent population, whereas the present trend infers that selection is within an F2 population of a cross of two pure lines. Pedigree selection, however, can be imposed on any type of population.

There are many options within each phase of a pedigree selection program: type of source populations, types of seasons for inbreeding lines, emphasis on selection among traits, selection intensity in each generation, and generation to evaluate lines in replicated trials. In maize breeding, decisions also are needed relative to the generation of inbreeding at which to begin tests for combining ability, and the choice of testers for measuring combining ability of lines. The sequence of activities for pedigree selection are outlined in Table 8-3. The suggested activities and numbers of progenies included each generation will vary among breeders. Although specifics will vary, the relative numbers suggested in the outline represent a consensus of U.S. maize breeders (Bauman, 1981).

The objective of pedigree selection in maize is to develop pure-line genotypes that are used as parents of hybrids. Accurate records are essential to maintain the filial record (pedigree) of each genotype during each generation of inbreeding and selection.

Backcrossing

Development of lines by the backcross method of breeding is probably used more frequently than any other method, except pedigree selection.
Table 8-8  Agronomic Performance for Four Inbred Lines Extracted from Iowa Stiff Stalk Synthetic (BSSS) Evaluated in Single Crosses with Mo17, an Elite Inbred Line Tester*

<table>
<thead>
<tr>
<th>Single Crosses</th>
<th>BSSS Source</th>
<th>Year of Release</th>
<th>Yield†</th>
<th>Grain Moisture</th>
<th>Lodging Root</th>
<th>Lodging Stalk</th>
<th>dropped Ears</th>
</tr>
</thead>
<tbody>
<tr>
<td>B14 × Mo17</td>
<td>C0</td>
<td>1953</td>
<td>70.8 q/ha</td>
<td>20.4%</td>
<td>12.3%</td>
<td>7.5%</td>
<td>1.1%</td>
</tr>
<tr>
<td>B37 × Mo17</td>
<td>C0</td>
<td>1958</td>
<td>76.3</td>
<td>22.5</td>
<td>17.3</td>
<td>16.4</td>
<td>1.2</td>
</tr>
<tr>
<td>B73 × Mo17</td>
<td>C5</td>
<td>1972</td>
<td>83.1</td>
<td>22.2</td>
<td>15.7</td>
<td>9.4</td>
<td>1.7</td>
</tr>
<tr>
<td>B84 × Mo17</td>
<td>C7</td>
<td>1978</td>
<td>93.6</td>
<td>22.6</td>
<td>11.9</td>
<td>10.8</td>
<td>0.9</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
<td>81.0</td>
<td>21.9</td>
<td>14.3</td>
<td>11.0</td>
<td>1.2</td>
</tr>
<tr>
<td>LSD (0.05)</td>
<td></td>
<td></td>
<td>3.8</td>
<td>0.5</td>
<td>4.8</td>
<td>3.8</td>
<td>—</td>
</tr>
</tbody>
</table>

*33 location-year environments.
†Yield: B84 > B73 > B37 > B14A = 12.6%, 8.9%, 7.8%. 
Backcrossing is usually used in the context of transferring a trait from one genotype (donor parent) to an otherwise desirable genotype (recurrent parent). The trait being transferred is usually simply inherited. Backcrossing is usually a correctional breeding method that is used to enhance the performance of an elite inbred line, but it also is used to insert a specific gene in an elite inbred line.

An example for a specific gene involves the transfer of the liguleless allele \( L_{g3} \) from a donor parent to recurrent parent. \( L_{g3} \) is a dominant allele and can be phenotypically identified among individual plants at flowering, and the expression of the \( L_{g3} \) allele is not affected by the environment. Such a trait can be easily transferred because the plants with the desired allele can be identified at the time of flowering. For other traits, the principles of backcrossing remain the same, but the mechanics of making the crosses, identification of plants with the allele being transferred, and the masking effects of the environment may be more difficult.

Other traits considered in a backcross program may be controlled by multiple genes. B14 is an elite inbred line that was used in hybrids, but it is highly susceptible to the European corn borer. An exotic source (41.2504B) possessed alleles for resistance to the insect, but it was not of any value itself for use in hybrids. It was desired to incorporate the resistance of 41.2504B into B14. Because of the quantitative nature of resistance to the European corn borer, it was necessary to include one or two generations of intermating of resistant plants and their progenies between generations of backcrossing to maintain acceptable levels of resistance. Use of conventional backcross breeding, as conducted for a qualitative trait, was not successful because the level of resistance decreased with successive generations of backcrossing.

Backcrossing can be completed in a relatively short time for certain traits. Lines converted for simply inherited traits can be completed in 3 to 5 years with the use of off-season nurseries. For more complex traits, a greater number of seasons will be required. In some instances, conversion of lines is not complete until they have been retested in hybrids to determine if line performance was changed in the backcrossing program.

FIELD-PILOT TECHNIQUES FOR GENOTYPE EVALUATION

Cultivars that have high, stable yield performance over environments are the ultimate goal of maize breeding programs. This goal often is elusive and can be frustrating because the chances of developing superior lines that meet modern production standards are indeed very low. This, in part, is why pedigree selection is emphasized in \( F_2 \) populations developed from elite lines. The chances of modifying elite lines by pedigree selection while maintaining standards of productivity are greater than attempting to
develop new elite lines from sources that have not had extensive testing. This is why germplasm of the elite inbred lines C103, B14, B37, B73, and Oh43 are prominent in the pedigrees of many modern hybrids. The primary objective of breeding is to develop hybrids that are better than those currently grown. Although major emphasis is given to evaluation of hybrids, stability of production of parental lines also is needed to have reliable production of single-cross hybrids.

It was understood early in the development of the inbred-hybrid concept that replicated trials were critical to identifying superior hybrids. Consequently, experimental-plot techniques and statistical analyses have received considerable attention by maize breeders. Maize breeders have been leaders in developing experimental procedures for testing and evaluating large numbers of entries.

The first evaluation stage in hybrid breeding programs is determination of the relative general combining abilities of new lines (Sprague and Tatum, 1942). At this stage, precise comparisons are not made. The first evaluation provides preliminary information from testcross data that is used in selection of lines that merit further consideration for inbreeding and selection. The consensus among maize breeders is that the initial testcrosses should be evaluated with use of two to three replications at four locations for 2 years (Bauman, 1981). On the average, therefore, 16 to 24 replications of testcross data are desired to discriminate among new lines as to their future potential for continuing in the breeding and testing program. Useful information on the resources required to detect differences for different types of hybrids and combinations of locations and years was provided by Federer and Sprague (1947).

After the lines have survived selection in the breeding nursery and showed promise in the initial testcrosses, the next stage is to test specific single crosses. It is not possible or necessary to test all possible single crosses among a group of new lines. Because of the heterotic patterns that have been identified, lines of 'Reid Yellow Dent' origin tend to be crossed with lines of 'Lancaster Sure Crop' origin in the U.S. Corn Belt. For example, lines extracted from a population improvement program involving 'Reid Yellow Dent' may be crossed with lines identified by pedigree selection in a population with 'Lancaster Sure Crop' germplasm. The most common procedure, however, is to test new lines with elite lines that currently are used in hybrids. The rationale is that a new line may be found that can be used with the elite inbred tester to produce a superior hybrid.

Testing of new hybrid combinations can be very extensive, particularly for private breeding programs. Seed firms cannot afford to produce and sell hybrids unless they have proven performance. Multistage testing is conducted, ranging from evaluation of experimental combinations to precommercial hybrids. Resources allotted to testing new single-cross
combinations are similar to those used in the initial testcross evaluation for combining ability. Hybrids that survive the initial trials are continued in expanded trials conducted over time and space. Seed supplies of potentially new hybrids are increased to permit additional testing. In addition to the local area where the new lines were developed, trials also are conducted over greater areas to determine the range of possible use and stability of performance over a range of different environments. Lines developed in central Illinois, for example, may be tested throughout the central U.S. Corn Belt from Nebraska to Ohio.

Sprague and Federer (1951) analyzed data of testcrosses, single-cross hybrids, and double-cross hybrids collected over locations and years. The objectives of the study were to estimate the relative importance of interactions of the three types of crosses with locations and years and determine the most efficient allocation of resources to maximize genetic gain and minimize costs. Single crosses were more variable among environments than double crosses, and single crosses had greater interaction variances with environments than double crosses. Expected genetic advance was greater by increasing locations and years rather than by increasing the number of replications at a limited number of environments. Their results suggested that for cultivar evaluation, the optimum distribution of a given number of plots, disregarding costs, was one replication per test site with a maximum number of locations and years. Based on costs per plot, however, this would be the most expensive allocation of replications because costs per plot decrease with increased replication per test site. Most breeders use at least two replications at each test site. If the number of plots per test site is 400 or more, increased gains in genetic advance can be realized without a disproportionate increase in cost per cultivar. Sprague and Federer (1951) presented tables for the optimum allocation of resources in maize trials.

Plot size and shape depends on soil variability, the precision required to detect differences among genotypes and the type of plot equipment used for planting and harvesting. Plots generally are longer than their width, and usually one to three rows are included in a plot. The trend for the past 40 years has been to use smaller plots, but there has been some increase in length the past 10 years to accommodate use of mechanical harvesting equipment. Plot size with a 1-m row spacing in the early years of maize breeding ranged from 12 m² (1 row × 12 m) to 20 m² (2 rows × 10 m). At the present time, a 0.75-m row spacing is common, and plot sizes range from 8.25 m² (2 rows × 5.5 m) to 9.15 m² (2 rows × 6.1 m). The most commonly used plot size includes two rows spaced 0.75 m apart and about 6 m long. Hallauer (1964) obtained estimates of soil variability from maize trials conducted in Iowa and calculated plot sizes necessary to detect differences among genotypes with different numbers of replications.
He concluded that eight replications would be acceptable for initial testing with a plot size of 8.25 m².

Interplot-competition effects among cultivars in small-plot trials can occur. If cultivars of different maturity and plant height are in adjacent plots, the earlier, smaller cultivars will be at a disadvantage in comparison with the later, taller cultivars. The effects of interplot competition usually are kept to a minimum by grouping hybrids in a test by maturity and plant type. If large differences among cultivars are known for plant height within the same maturity, three or four-row plots are used and data are collected from the center rows. If the differences among hybrids are not known in advance, biases in estimates of cultivar means will occur.

Intraplot competition also can occur, the extent of which will vary among the types of cultivars evaluated. Eberhart et al. (1964) studied intraplot competition among single crosses and detected significant microenvironment × genotype interactions. In pure stands of single crosses, intraplot competition existed, but it was of the compensating type. Intraplot competition effects, therefore, would not affect comparisons among single-cross hybrids.

Randomized complete-block and lattice designs are the most frequently used experimental designs for estimating cultivar means. The choice of designs is determined by number of cultivars included in the experiment, soil variability at the experimental sites, the stage of cultivar testing, and facilities for data analysis. Past experience also may influence the types of design used in certain situations. Simple lattice designs are frequently used in early stages because usually 100 or more cultivars may be under test and seed supplies may be limited.

Decisions about the choice of an experimental design can be made by comparing their relative efficiencies. If the lattice design is efficient in reducing the experimental error by a certain amount, generally about 10%, the lattice design is used rather than the randomized complete-block. Because some environmental effects are unpredictable, the efficiency of lattice design may not be known in advance. A procedure used by some programs is to always use a lattice design, calculate the analysis of variance, and compare its relative efficiency to a randomized complete-block design. If efficiency of the lattice is less than some specific value, further analysis is based on a randomized complete-block design. Blocks within sets, augmented, and split plot designs are used in specific instances, but not as frequently as the lattice and randomized complete-block.

Development of computer hardware and software has permitted more extensive analysis of performance data in recent years. In addition to the standard analyses of variance and mean calculations, yields may be adjusted for differences in stand and maturity. Stability of performance also
is important, and parameters measuring response to environments and relative stability over environments can be estimated routinely (Eberhart and Russell, 1969). Correlations between traits are computed for some specific studies, but generally not among elite cultivars. Components of variance can be estimated from analyses of variance to estimate the coefficient of variation, the relative variation among cultivars tested, and the heritability or repeatability of the materials tested.

Development of mechanical equipment adapted for use on small experimental plots has occurred within the past 15 years. Before 1970, most field trials were conducted with manual labor. Today, nearly all field trials are conducted with use of mechanical equipment. Mechanical equipment was developed from three sources: (a) specific small-plot equipment developed and built by firms that specialize in custom-made experimental equipment; (b) simple modifications of commercial equipment for use on small experimental plots; and (c) integration of specific commercial equipment with custom-made equipment. The choice of equipment depends on personal preferences, although modifications of commercially available equipment has been the most popular because they often cost less. Refinements have been made to improve the efficiency and accuracy of planters and harvesters, and new modifications are made regularly to improve the distribution of seed by planters, weighing of grain, and the determination of test weight and moisture of grain. Electronic data collectors are being adapted to enhance the transfer of field data to the mainframe computer. Specialty equipment for determining stalk strength, root strength, and moisture content of an ear attached to a plant are available from specialty equipment firms.

There is one type of hybrid test that is unique to the commercial seed industry. It is the on-the-farm strip tests conducted for precommercial and commercially produced hybrids. Strip tests are usually nonreplicated and have larger plots (0.25 to 0.5 ha) than those commonly used for experimental trials. They are planted and harvested by the farmer with the same equipment used for commercial maize production. The main objectives of the strip tests are to determine how the hybrids perform under farm conditions and to provide additional information in determining whether a hybrid should be considered for large-scale production. Strip tests are usually limited to the final stages of hybrid evaluation.

PROCEDURES FOR SEED PRODUCTION

Seed production is primarily a function of private seed firms. Since it became apparent that farmers would accept the practice of purchasing good quality hybrid seed each year, the commercial hybrid maize seed in-
Industry has developed from a few family-owned businesses to large multimillion dollar corporate firms, which market seed internationally. There are about 300 firms that market hybrid seed in the United States.

**Methods for Producing and Maintaining Seed Stocks**

The maize breeder identifies inbred lines that produce hybrids that are better than currently used hybrids. After the preliminary trials suggest that an inbred line has potential, the breeder increases the seed supplies of the inbred line and produces larger quantities of hybrid seed for expanded testing. Seed of the line at this stage of development is usually referred to as breeder seed because the breeder is responsible for maintaining purity and increasing seed supplies of the line. Breeder seed is obtained by hand self-pollination.

The production of hybrid seed required for performance trials usually is the responsibility of the breeder. Cross pollinations usually are made by hand in breeding nurseries to produce the new hybrid. Both the breeder seed and hybrid seed increases can be done by natural cross-pollination in isolated nurseries, but there may be too many lines and experimental hybrids at this time to justify the cost of the isolations. Seed purity is maintained by roguing off-type plants and using careful pollination techniques. The methods and techniques are similar for both private and public programs at this stage.

Lines that have survived selection after extensive testing in hybrids must be increased to provide adequate quantities for hybrid seed production. If selected hybrids are considered precommercial or are in advanced hybrid trials, they are approaching the stage at which they are serious candidates for commercial production.

Production of large quantities of seed of inbred lines is handled by foundation seed stock organizations in both public and private programs. The production occurs in isolation plantings, which are located not closer than 200 m from maize of a different color and texture. The size of isolations will depend on the seed yield of the lines. Isolations are checked for off-type plants and carefully rogued to eliminate possible contaminants. Breeders are not directly involved in this phase of seed production, but they may be consulted if some specific problems or questions arise relative to plant type and reaction to certain pests and environmental effects.

If new lines are developed in public programs and have potential as parents in commercial hybrids, they are made available for use by private and other public programs. The private companies will increase seed supplies without restrictions on future use of the line for hybrid seed production.
Commercial Seed Production and Marketing

Production and marketing of hybrid seed is self-regulated in the United States. Poor quality seed and hybrids with inconsistent performance are not tolerated by commercial growers. Competition for future sales ensures that a good product is provided at a competitive price. Private companies conduct research relative to seed production, harvest, handling, processing, quality, and storage to develop efficient methods of providing high-quality hybrids seed. Firms may have genetically superior hybrids, but if poor production and handling methods are used, the genetic potential of hybrids will not be realized. Although most production and processing methods are regulated by the company, most firms also have independent agencies that audit their techniques. State certification agencies are employed to inspect production fields for proper isolation standards, pollen control, and roguing of off-types plants. Samples of seed anticipated for sale are sent to independent seed laboratories to examine them for seed damage, presence of seed pests, and germination under cold and warm conditions. Results of inspections and tests are compared with their own information to determine if they are using adequate methods of quality control. In many countries, tests of purity of seed parents and purity and performance of hybrids are required by governmental agencies before firms are permitted to offer the seed for sale. The seed firms must provide evidence that the new hybrids are unique and have acceptable performance. The stringency of the requirements varies among countries.

Methods of marketing hybrid maize seed range from sale by government agencies in socialist countries to farmer dealers in the United States. There are combinations of these two extremes in various countries. The marketing method currently used in the United States evolved from the techniques first used in the 1930s for the sale and distribution of hybrid seed to farmers. Although firms have regional, district, and area sales managers, the direct sale, handling, and distribution of seed is usually at the farmer-dealer level. Highly selected, progressive farmers that have visibility within a community are provided the opportunity to sell seed to their neighbors. Commissions obtained by the farmer for seed sales supplement the regular farm income. Seed is offered for sale in units that vary in size among firms and occasionally for hybrids within firms. The type of unit offered for sale of a specific hybrid is related to the level of difficulty in producing the hybrid seed. Initially, nearly all units were 25.4 kg (1 bu) in the United States, but in recent years, hybrid seed may be offered in units of 22.7 kg (50 lb), 25.4 kg (56 lb), or number of viable kernels (e.g., 80,000). In other countries, units of hybrid seed offered for sale may vary from 1 to 30 kg.

Hybrid seed production and marketing is a highly technical and com-
petitive industry. Improved methods of seed production are changing as
the technology is developed. Reviews of the details of hybrid seed
production were given by Craig (1977) and Wright (1980).

FUTURE PROSPECTS FOR CULTIVAR DEVELOPMENT

Evidence suggests that substantial genetic gains have been realized by the
methods of maize breeding currently used in the United States (Russell,
1985). There is some question as to whether the past rates of gain can be
continued in the future. Circumstantial evidence suggests that they can.
Although maize yields are affected by the vagaries of the environment,
there is no evidence to expect a decrease in the rate of genetic gain in the
near future.

An indication that hybrid yields will continue to increase is suggested
by the comparative yields obtained from hybrids grown under good man-
agement versus the average yields for Iowa (Fig. 8-4). These trends relate
to differences in husbandry rather than genetic changes, but the hybrids
must have the genetic potential to respond to better cultural and manage-
ment situations. The data included in Fig. 8-4 compare the yields obtained
by contest winners and the state average for 4.0 to 5.6 million ha of maize
production. Farmers voluntarily enter the contests to determine which indi-
vidual can harvest the greatest yield. All contest fields that report yields
that exceed 112.5 q/ha are verified by an independent referee. The data
are from 1954, when machine harvested plots were first measured, to
1984. The increases for yield were nearly parallel for the contest and state
average. But the yield of the contest plots was nearly 60 q/ha greater than
the state average. The rates of yield increase for the 30-year period were
1.31 q/ha for the state average and 1.56 q/ha for the maize contest. If the
rates of yield increase for the past 30 years are projected to year 2000, the
predicted state average yield is 96.1 q/ha for Iowa and 165.6 q/ha for the
maize contest. In both instances, the yield levels have continued to
increase because of better hybrids, better cultural practices, and better
management.

Genetic variability is the essential ingredient for successful breeding
programs. Cumulative evidence from quantitative genetic studies and
selection experiments suggest significant amounts of additive genetic
variability are present to provide continued progress (Hallauer and
Miranda, 1981). The progress achieved in the United States was from the
use of less than 5% of the maize germplasm available to the breeders
(Brown, 1975). Although it does not seem genetic variability is a limiting
factor for continued genetic gains at the present time, a tremendous reser-
voir of germplasm is still available if a leveling-off in response to selection
does occur. Most of the germplasm is not adapted and, consequently, is
not directly usable in U.S. Corn Belt breeding programs. Hence,
Figure 8-4  Yield of winners of the Iowa master maize contest, average yields in Iowa, and the linear yield response for contest winners and the state average for 1954 to 1984 (Russell, 1985). ○ corresponds with the Iowa winners (left-hand scale); ⬤ corresponds with the Iowa average (right-hand scale).

maize breeders need to introduce, adapt, and evaluate the germplasm to have it available for future use (Goodman, 1985).

Another factor that will contribute to maintaining genetic gains is the tremendous expansion in private breeding and testing programs over the past 30 years. The level and intensity of these programs will provide elite inbred lines and hybrids that have survived extensive selection and testing. The programs include materials in various stages of development that should provide superior hybrids in the future.

REFERENCES


