

1988

Corn Breeding

A. R. Hallauer

U.S. Department of Agriculture, hallauer@iastate.edu

Wilbert A. Russell

Iowa State University

K. R. Lamkey

U.S. Department of Agriculture, krlamkey@iastate.edu

Follow this and additional works at: http://lib.dr.iastate.edu/agron_pubs



Part of the [Agricultural Science Commons](#), [Agronomy and Crop Sciences Commons](#), and the [Plant Breeding and Genetics Commons](#)

The complete bibliographic information for this item can be found at http://lib.dr.iastate.edu/agron_pubs/259. For information on how to cite this item, please visit <http://lib.dr.iastate.edu/howtocite.html>.

This Book Chapter is brought to you for free and open access by the Agronomy at Iowa State University Digital Repository. It has been accepted for inclusion in Agronomy Publications by an authorized administrator of Iowa State University Digital Repository. For more information, please contact digirep@iastate.edu.

Corn Breeding

Abstract

Corn (*Zea mays* L.) breeding for hybrid development was begun in the early 1900s with the work of Shull (1909), East (1908), and others, but a primitive type of breeding was conducted for thousands of years by the American Indians before the European colonists began settlement in the New World. The U.S. Corn Belt dents were derived from crosses that included germ plasm of the northeastern flint and southern dent or gourdseed types, beginning about 1850, with subsequent selection that developed the U.S. Corn Belt dents. Open-pollinated cultivars, such as Reid Yellow Dent, Krug, Learning, and Lancaster Sure Crop were developed by a type of mass selection that was based on plant, ear, and grain type. This early work, which was done primarily by farmers and seedsmen, provided the germplasm sources from which were developed the inbred parental lines that were used to produce the first double-cross hybrids used in the USA. Even to the present time, relatively little germ plasm from other countries has been used in corn breeding programs in the USA (Brown, 1975).

Disciplines

Agricultural Science | Agronomy and Crop Sciences | Plant Breeding and Genetics

Comments

This is a chapter from Haullauer, A. R., W. A. Russell, and K. R. Lamkey. 1988. Corn Breeding. In G. F. Sprague and J. W. Dudley (eds.) Corn and Corn Improvement. Agronomy 18:463-564. Am. Soc. of Agron., Madison, WI. Posted with permission.

Rights

Works produced by employees of the U.S. Government as part of their official duties are not copyrighted within the U.S. The content of this document is not copyrighted.

8

Corn Breeding¹**A. R. HALLAUER***USDA-ARS**Ames, Iowa***WILBERT A. RUSSELL***Iowa State University**Ames, Iowa***K. R. LAMKEY***USDA-ARS**Ames, Iowa*

Corn (*Zea mays* L.) breeding for hybrid development was begun in the early 1900s with the work of Shull (1909), East (1908), and others, but a primitive type of breeding was conducted for thousands of years by the American Indians before the European colonists began settlement in the New World. The U.S. Corn Belt dents were derived from crosses that included germ plasm of the northeastern flint and southern dent or gourd-seed types, beginning about 1850, with subsequent selection that developed the U.S. Corn Belt dents. Open-pollinated cultivars, such as Reid Yellow Dent, Krug, Leaming, and Lancaster Sure Crop were developed by a type of mass selection that was based on plant, ear, and grain type. This early work, which was done primarily by farmers and seedsmen, provided the germplasm sources from which were developed the inbred parental lines that were used to produce the first double-cross hybrids used in the USA. Even to the present time, relatively little germ plasm from other countries has been used in corn breeding programs in the USA (Brown, 1975).

Breeding procedures were used to improve and develop new strains of the open-pollinated cultivars in the late 1800s and early 1900s before the development of inbred lines for hybrid seed production was begun. These breeding procedures included varietal hybridization, mass selection, and ear-to-row selection. Descriptions of the procedures have been published in earlier years, and results from a few studies were summarized by Sprague and Eberhart (1977). These procedures were not successful to effect yield improvements. In some instances, varietal hybridization

¹Joint contribution of the USDA-ARS, and Journal Paper no. J-12562 of the Iowa Agric. and Home Econ. Exp. Stn., Ames, IA 50011. Project no. 2778.

gave crosses that produced better than the higher-yielding parent, but the procedure was not accepted widely for commercial use. Selection programs were successful in producing numerous strains that varied for maturity, plant type, ear and grain type, and pest resistance. Corn shows conducted at the start of the 20th century also caused selection for a distinct ear and grain appearance. Close selection to type, however, may have caused some inbreeding, which may have been the primary reason that yield improvements were not realized. Mass selection and ear-to-row selection were gradually discontinued as inbred development for hybrid use became the accepted method. Modifications to mass selection (Gardner, 1961) and ear-to-row selection (Lonnquist, 1964) have been used to enhance the effectiveness of these selection methods for improving yield in breeding populations.

Results of breeding studies by Shull, East, and Jones in the early 1900s led to the establishment of programs at many U.S. agricultural experiment stations and by the USDA for the development and evaluation of inbred lines and hybrids during the period of 1915 to 1925. Corn breeding as a private commercial enterprise came a few years later. It was the 1930s before farmer use of hybrid seed became an acceptable practice; hybrid corn occupied approximately 100% of the corn area in Iowa by 1943, 90% of the corn area in the U.S. Corn Belt, but only 60% of the corn area for the entire USA (Fig. 8-1). Double-cross hybrids were the predominant type in the USA until about 1960 when the use of single crosses began to increase. Single crosses became the predominant type in a few years, with considerably fewer hectares being planted to related-line single crosses, three-way crosses, and double crosses.

Corn breeding for the development of inbred lines and hybrids in other parts of the world expanded rapidly after World War II. Corn has proved to be a flexible species amenable to selection such that progress

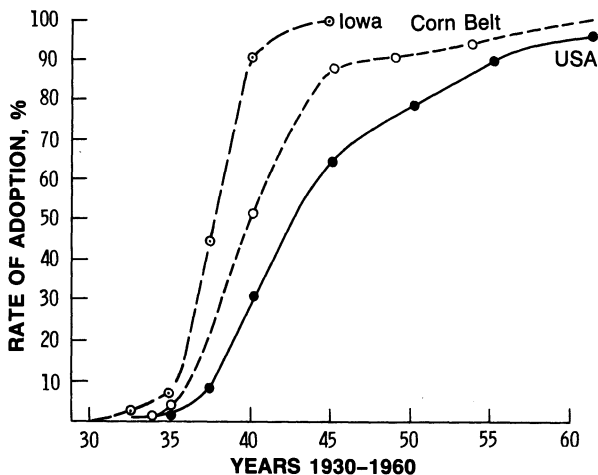


Fig. 8-1. Rate of acceptance of double-cross hybrids in Iowa, the U.S. Corn Belt, and the USA.

has been achieved to develop types adapted to many areas where it was not grown or was relatively unimportant in earlier years. An excellent example has been the tremendous expansion in some European countries, made possible by the selection of earlier maturity, better adapted cultivars that can be grown successfully in areas where such was not feasible 40 years ago (Trifunovic, 1978). Some inbred development and evaluation were done in a few European countries before 1940, and such programs were expanded greatly after 1945. In the first period of this expansion, materials from the USA were evaluated and some U.S. hybrids were used. Subsequently, European and U.S. lines in hybrid combinations were developed and these helped to expand the corn-growing area and to give higher yields. The European lines introduced greater cold tolerance and adaptation for earlier maturity and the U.S. lines added improved yield and standability. These combinations permitted the expansion of hybrid corn into central Europe. In France, for example, the hectareage has increased more than five times from pre-World War II to the present time, and France is now a leading corn producer in Europe. Corn has become the most important feed crop in southern and central Europe.

Corn ranks second to wheat in total production among the world's cereal crops (CIMMYT, 1984). World corn production now normally exceeds 400 million t. During the period 1970–72 to 1981–83, world corn production increased about 120 million t, which represents a 42% increase in the world supplies at a rate of 3.1% yr⁻¹. More than 50% of the total world area planted with corn is in Latin America, Africa, and south and southwest Asia, but probably <25% of the total grain production is in this area (Wellhausen, 1978). Hybrids are the primary type grown in Argentina, South Africa, and parts of Brazil, but the remainder of the area uses open-pollinated cultivars, improved synthetics, variety crosses, and hybrids. In some areas where corn grain is used primarily for human consumption, considerable work has been done to improve protein quality through the use of *opaque-2*. As the technology is improved, it seems likely that hybrid types will become more important in most of the tropical and subtropical areas.

Corn grain yields in the USA have increased from approximately 1.3 Mg ha⁻¹ in 1930 to 7.5 Mg ha⁻¹ in 1985 (Fig. 8–2). Before 1930, average yields were static because no yield gains were realized from breeding and essentially no improvement occurred because of changes in cultural practices. The mass and ear-to-row selection methods that breeders and seedsmen used before 1930 were not effective in yield improvement. Yield increases have occurred since mid-1930s because of the use of hybrids, increased use of fertilizers, better weed control, higher plant densities, and improved management. The rate of yield gain increased beginning about 1960 when single-cross hybrids gradually replaced double crosses. Also, there was a rapid increase in the use of N fertilizer during 1960 to 1970 (Thompson, 1986). Mean yields plotted in Fig. 8–2 show a greater variability among years for average yields in the 1970s, but there is no

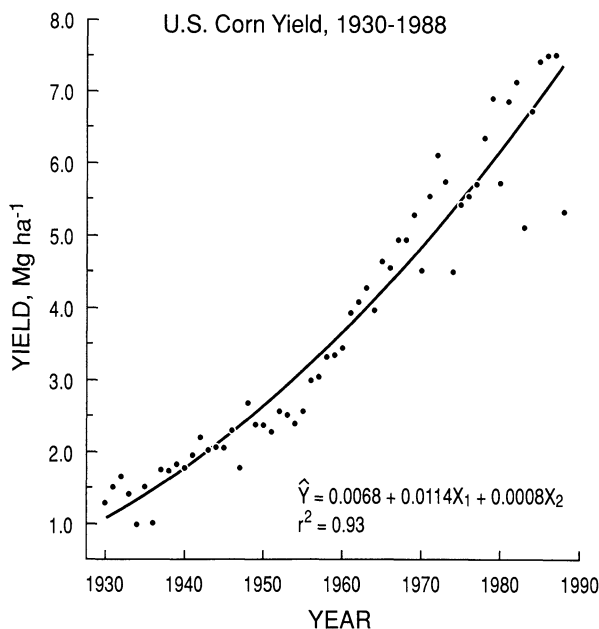


Fig. 8-2. National average of corn yields in the USA for the period including 1930-1988.

evidence of a plateau effect. Thompson (1975), by using a regression equation derived from corn yields and weather data in Illinois, predicted yields in that state would level off at 7.5 Mg ha⁻¹ by 1985.

Evidence for the contribution of breeding to corn yield increases has been obtained in several experiments (Russell, 1974, 1984, 1985a, 1986; Duvick, 1977, 1984; Crosbie, 1982; Tapper, 1983; Castleberry et al., 1984; Meghji et al., 1984). Most of these experiments included hybrids that were representative of materials grown from 1930s to 1970 or 1980; in a few studies open-pollinated cultivars from prehybrid times were included. Frey (1971) and Darrah (unpublished data reported by Hallauer, 1973) obtained estimates by using data from the Iowa Corn Yield Tests; all other data were obtained in experiments designed purposely to obtain information to assess genetic gains. A summary that includes total and genetic gains is given in Table 8-1. Total gains ranged from 0.078 to 0.110 Mg ha⁻¹yr⁻¹ and genetic gains were 0.033 to 0.092 Mg ha⁻¹yr⁻¹. The estimates, using open-pollinated cultivars as the basis for the proportion of total gain that was caused by genetic improvement, ranged from 56 to 89% for the planned experiments; some may be considered actual genetic gains whereas other estimates were biased because of harvest method. For example, the estimates of machine-harvested plots (see footnotes, Table 8-1) are likely biased in favor of newer hybrids because greater stalk lodging of the older hybrids would be expected to have caused greater harvest losses. The combined effects of improved cultural practices and better hybrids were confounded in these experiments. The hybrids have increased in yield because of their continued improvement in genetic potential to take advantage of improved cultural practices.

Table 8-1. Summary of 13 estimates of total grain yield gain and the genetic total yield gain of corn hybrids. (Table 3 from Russell, 1986). Adapted from Duvick (1984).†

Author	Year reported	Time span	Experiment yr	Total gain		Genetic gain	
				—	Mg ha ⁻¹ yr ⁻¹ —	—	%
Frey	1971	1926-1968	1926-1968	--	--	--	56
Darrah	1973	1930-1970	1930-1970	0.099	0.033	0.033	33
Russell	1974	1930-1970	1971-1973	0.078	0.063	0.063	79
Russell‡	1974	1930-1970	1971-1973	0.078	0.049	0.049	63
Duvick	1977	1935-1971	1972-1973	0.088	0.050	0.050	57
Duvick	1977	1935-1972	1972-1973	0.088	0.053	0.053	60
Tapper§	1983	1930-1970	1980-1981	--	--	--	42
Tapper§	1983	1930-1970	1980-1981	--	--	--	67
Castleberry et al.	1984	1930-1980	1980-1981	0.110	0.082	0.082	75
Duvick	1984	1930-1980	1978-1980	0.103	0.092	0.092	89
Duvick	1984	1930-1980	1977-1979	0.103	0.073	0.073	71
Russell	1984	1930-1980	1981-1982	0.090	0.071	0.071	79
Russell‡	1984	1930-1980	1981-1982	0.090	0.050	0.050	56

† Gains calculated basis U.S. corn yields by Castleberry et al. (1984); basis Iowa state yields for all other estimates.

‡ Adjustments made to estimate gains because of difference between experiment and Iowa state average yields.

§ Gains calculated relative to 1930-era hybrids; first estimate—total yields, second estimate—machine harvest yields.

The newer hybrids, 1970 or 1980, compared with hybrids of the 1930s had higher yields at all plant densities, and the differences generally were greater at higher plant densities. The newer hybrids had the genetic potential to take advantage of the higher number of plants per unit field area and, thus, to produce much higher yields than the older hybrids. The older hybrids generally had more barrenness at the higher plant densities than did the newer hybrids. Also, differences between the older and newer hybrids for lodging increased with higher plant densities, with the newer hybrids showing considerable superiority.

Castleberry et al. (1984) compared cultivars from six decades, 1930 to 1980, in low- and high-fertility conditions at one location for 2 yr. The high-fertility area had received normal fertilizer applications for 20 yr, whereas the low-fertility area had been in continuous corn and unfertilized since 1958. The higher fertility area received approximately 200 kg of N ha⁻¹, 90 kg of P₂O₅ ha⁻¹, and 150 kg of K₂O ha⁻¹ in 2 yr of test; the low-fertility area received no fertilizer. The yield response relative to decades of cultivars was 0.087 Mg ha⁻¹yr⁻¹ in the high-fertility condition and 0.051 Mg ha⁻¹yr⁻¹ in the low-fertility condition. The newer hybrids were superior to the older cultivars in both fertility levels, and the superiority was greater for the high-fertility area than for the low-fertility area.

Duvick (1984) evaluated four single crosses representative of four decades, 1940 to 1970, at low, intermediate, and high N levels. His newer hybrids outyielded the older hybrids at all N levels, but the hybrid × N level interaction was not significant. Carlone and Russell (1987) included

four cultivars from each of seven eras (pre-1930–1980) and evaluated them in 12 treatment combinations of three plant densities and four N levels. Grain yields showed that the treatments (plant densities and N levels) were interdependent, and the interaction of the two treatments varied among cultivars; i.e., the densities $\times$ N levels $\times$ cultivars interaction was statistically significant. The newer cultivars, 1970 and 1980 eras, were the highest yielding at all N levels, and each cultivar seemed to have a unique plant density-N level combination at which it produced a maximum yield. Differences among eras for N response showed no distinct patterns relative to the eras.

Improvement for resistance to root and stalk lodging, which was necessary to permit machine harvesting and the use of higher plant densities, was achieved. Selection for disease resistance has been an integral part of corn breeding for many years, yet there are little data that reflect directly on the effect of greater resistance to grain yield. Improvement for stay-green, which is primarily a visual rating for plant health, has been well documented (Duvick, 1984; Tapper, 1983; Meghji et al., 1984; Russell, 1985a), and stalk quality is dependent upon total plant health. Stay-green may also reflect improvement for resistance or tolerance to second-generation European corn borer [*Ostrinia nubilalis* (Hübner)]. Duvick (1984) showed a continuous improvement in the resistance to second-generation European corn borer from the 1930 to the 1980 hybrids, which would be conducive to greater stalk quality and reduced harvest losses.

The commercial use of single-cross hybrids has been made feasible by improvement of parental inbred lines. Agronomic improvements include cold tolerance such that germination and emergence are better, resistance to plant diseases and insects, resistance to barrenness, resistance to lodging, better pollen production, higher seed yield, and better seed quality. Duvick (1984) found that 1970 inbreds compared with 1930 inbreds had a yield gain of $0.05 \text{ Mg ha}^{-1}\text{yr}^{-1}$, or a total predicted gain of 2.0 Mg ha^{-1} . Meghji et al. (1984) obtained no yield increase for 1950-compared with 1930-era inbreds, but the 1970-era inbreds had an average yield increase of 14.5% over the 1950 lines. Furthermore, the 1950- and 1970-era inbreds were improved for plant health and resistance to lodging compared with the 1930 inbreds. Whereas in earlier years breeders selected lines primarily on the basis of hybrid performance, now more emphasis is given to the development of lines that have greater vigor and, thus, higher seed yields.

Yield increases in other corn-growing countries began later than in the USA partly because improved cultivars, including hybrids, were not generally used until after World War II. For Europe, the estimated yield increase per hectare was 2.4-fold for 1969 to 1973 over 1934 to 1938 (Trifunovic, 1978). In France, the yield increase per hectare was 3.2-fold for the same period. These increases occurred because of both improved cultivars and better field husbandry. Wellhausen (1978) reported that a

double-cross hybrid released in Brazil in 1958 yielded approximately 50 and 58% better than 'Paulista' and 'Cateto', respectively, the two most common races grown in Brazil in earlier years. Kuhn and Gevers (1980) found for 2 yr, in South Africa 1977/78 and 1978/79, that the best hybrids yielded 41.2% above the mean for the first hybrids released. Most of the increase in world corn production was achieved by yield improvement. In developing countries, yields increased $2.6\% \text{ yr}^{-1}$ while the area planted increased $1\% \text{ yr}^{-1}$ (CIMMYT, 1984).

Further increases in corn yields are expected primarily because of the combined effects of two factors: (i) improved cultural practices and management and (ii) increased genetic potential of the hybrids. The rate of genetic gain for grain yield could become even greater than shown previously because there are now more breeders and companies with breeding programs. It seems likely further gains will be achieved by the development and evaluation of parental materials at higher plant densities. Stalk lodging will be a problem and must be corrected if higher plant densities are to be used. Recurrent selection can be used effectively to improve stalk quality in breeding populations, but must be done with yield evaluation to avoid yield declines (Devey and Russell, 1983; Martin and Russell, 1984a, b). Genetic engineering techniques have not yet had an impact on corn improvement, but effects for some aspects of corn improvement may be realized in the near future. Also, we have only just begun to explore in greater depth the possible utilization of germ plasm from other areas.

8-1 BREEDING METHODS

8-1.1 Methods for Line Development

The essential features of the inbred-hybrid concept used in corn breeding were eloquently described by Shull (1908, 1909, 1910). The major focus of corn breeding programs is the same as that stated by Shull (1909) "... the object of the corn breeder should not be to find the best pure line, but to find and maintain the best hybrid combination." Shull's suggestion was not immediately accepted because of the practical concerns of producing adequate quantities of hybrid seed at an acceptable cost. These concerns were alleviated with Jones' (1918) suggestion that single crosses be used as parents to produce double crosses rather than inbred lines used to produce single crosses, as suggested by Shull (1909). Hence, the basis for producing and growing hybrid corn was in place by 1920. During the 1920s, the USDA, state agriculture experiment stations, and individuals initiated corn breeding programs to develop and test inbred lines and hybrids. Agencies and individuals responded to Shull's

(1910) plea that, "My anxiety is not for success of the pure-line methods outlined by myself, but that serious experimentation shall be undertaken by every station within the corn-growing region for the purpose of discovering what is the best method."

8-1.1.1 Pedigree Selection

Pedigree selection is the most widely used breeding method to develop inbred lines for use as parents of hybrids. The types of populations sampled, methods of selection used, and the emphasis given to traits during selection have changed, but the basic principles of pure-line development are used. Initially, pedigree selection was practiced in the open-pollinated landrace cultivars that were adapted to the areas in which the breeding programs were located. Useful inbred lines (e.g., L317, L289, I205, Os420, WF9, etc.) were developed from the landrace cultivars, but it soon became obvious that repeated samplings of the same landrace cultivars were not productive. A logical sequel was to cross pairs of elite inbred lines that complemented one another, produce the F_2 generation, and practice pedigree selection by sampling the F_2 population. F_2 populations of single crosses are the most frequently (37%) used source populations for line development (Bauman, 1981). Other populations frequently used by U.S. breeders to initiate pedigree selection include genetically broad- (15%) and narrow-base (16%) populations improved by selection for specific traits, and populations (14%) formed by intermating elite inbreds that may be either related or unrelated (Bauman, 1981). The choice of germ plasm depends on the breeding objectives, stage of development of breeding program, and germ plasm available.

The scheme of the pedigree selection program depends on the skills of the individual breeder, primary breeding goals, the resources available for advancing the progenies, intensity of selection, and scope of testing. Different breeders emphasize selection for different traits because of locally important pests at different stages of inbreeding. The intensity of selection will vary, depending on the effective screens available for pests, environments available, and types of material under selection. One common feature, however, is that records are kept for each progeny for the traits selected for each generation of inbreeding.

Adequate sample sizes of the source breeding populations are necessary to include the range of possible segregants. In most instances, however, it is not possible to have a sample size that includes the theoretical number of possible genotypes for the segregating loci. If, for example, the cross between two parents differed for five allelic pairs, the smallest theoretical F_2 population would require 1024 individuals; if the parents differed for 10 allelic pairs, the theoretical F_2 populations would include 1 048 576 individuals. Most of the traits emphasized in selection of lines are controlled by more than five genetic factors, and, therefore, compromises are made for sample sizes because the breeder usually is sampling more than one population. Generally, the decision on sample

size depends on the heritability of the trait to be improved and(or) the experience of the breeder making the selections among progenies. Bauman (1981) reported there was great variation among the initial sample sizes, with sample size of 500 being the more common. After the initial sampling, the number of progenies surviving in subsequent generations of inbreeding (without testcross evaluation) was quickly reduced. The idealized number of surviving progenies after sampling 500 plants (S_1 progenies) was reported by Bauman (1981) to be 180 in the S_2 generation, 80 in the S_3 generation, and 40 in the S_4 generation. Average selection intensities were 63, 56, and 50% in the S_1 , S_2 , and S_3 generations, respectively, for visually selected traits. The breeders preferred use of smaller sample size in a greater number of populations rather than greater sample size in one or two populations.

The general procedure with use of F_2 populations is to initiate selection and selfing without any genetic recombination. The breeder usually has a mental image of the ideotype desired, and, depending on the skill of the breeder, desirable ideotypes of the favorable parent can be recovered with slight modifications. Favorable linkages would be desirable in these instances. The effects of random mating within F_2 populations before sampling are not conclusive. Pederson (1974) and Bos (1977) have presented theoretical arguments against random mating in F_2 populations of self-pollinating species. Altman and Busch (1984) reported there was insufficient useful recombination to justify random mating single-cross populations of wheat (*Triticum aestivum* L.) before initiating selection. Humphrey et al. (1969) in tobacco (*Nicotiana tabacum* L.) and Nordquist et al. (1973) in sorghum [*Sorghum bicolor* (L.) Moench] reported random mating increased genetic recombination which provided desirable recombinants.

Empirical data for random mating single crosses of corn before conducting pedigree selection are limited. Covarrubias-Prieto (1987) estimated the variability among 100 S_1 progenies in F_2 populations of B73 $\times$ Mo17 (cross of unrelated lines) and B73 $\times$ B84 (cross of related lines) and after five generations of random mating 250 plants in each F_2 population. Objectives of the study were to determine if random mating was effective for increasing genetic variability in populations formed from single crosses and if the relatedness of the inbred lines used to make the cross was an important consideration for random mating. Preliminary evidence suggests that random mating did not increase genetic variability in either F_2 population. Estimates of the S_1 components of variance were similar for the F_2 and F_2 random mated six times. Indirect evidence suggests that selection and intermating are effective via use of recurrent selection procedures (e.g., B14, B37, B73, and B84 derived by pedigree selection from cycles of selection in BS13).

Pedigree selection will always be an important component of modern corn-breeding programs. Based on surveys by Hallauer (1979) and Bauman (1981), it seems pedigree selection will be emphasized in populations

with a restricted genetic base. Because of the availability of elite lines and competition among private companies to provide high-performance hybrids, germplasm sources that include favorable linkages will be used to increase the odds of recovering elite lines and hybrids. The skills of the breeder in selection and the precision of testing have been found effective for developing improved lines and hybrids by pedigree selection (Duvick, 1977; Bauman, 1977). Except for germplasm sources, the methods of selection and hybrids currently produced and grown are those described by Shull (1909, 1910).

8-1.1.2 Backcrossing

Backcross method of breeding is a modification of the pedigree method and is an important component of most breeding programs. Bauman (1981) reported that 17% of the total effort for inbred line development was allocated to backcross sources. The main difference between backcross and pedigree selection is in the objective of the crosses and the level of recovery of the recurrent parental genotype. The complexity of the backcross method depends on type of trait being transferred (single gene vs. several genes), level of expressivity, whether cytoplasmic or nuclear inheritance, and the types of parents included in the crosses. For single gene traits that are relatively easy to classify, the backcross method is effective and relatively easy to manage. For traits that have a more complex inheritance, the backcross method requires greater selection pressure for the desired trait, but it has been successfully used to transfer traits in which the effects of individual genes were not known (e.g., Duvick, 1974).

Modifications of the backcross method have been suggested. Convergent improvement was a concept developed by Richey (1927) for the parallel improvement of two inbred lines by the reciprocal addition of dominant favorable genes present in one line but lacking in the other line. Richey and Sprague (1931) and Murphy (1942) presented experimental evidence that convergent improvement was effective for yield improvements of the recovered lines and their respective single crosses. However, convergent improvement is apparently not an important component of current breeding programs.

For traits that have a more complex inheritance, usually some modifications are needed to transfer the trait effectively. Bailey (1977) and Johnson (1980) presented formulae and examples of the probabilities of recovering more than “n” loci with “x” favorable alleles. Their theoretical calculations, based on F_2 populations where $p = q = 0.5$ for segregating loci, support the experiences in breeding. If the trait being transferred has a high heritability (nearly 100%) for a trait, such as *Ht* conditioning resistance to *Helminthosporium turcicum* Pass. (Hooker, 1961), the chances of recovering the favorable alleles of the recurrent parent are good with successive backcrosses. Tight linkages of unfavorable alleles with the gene being transferred from the donor parent would, of course, affect the outcome in an obvious manner (Bailey and Comstock, 1976).

If the trait is conditioned by 20 genes, has a heritability of 0.50, and a 10% selection intensity is used, Bailey (1977) showed that the probability of obtaining a recovery with 80% of the favorable alleles was 0.271 in the second backcross. The greater the number of loci, the lower the probabilities in recovering all of the favorable alleles. Johnson (1980) concluded that, the more divergent the parents in making the crosses, several backcrosses to the better parent will be required to enhance the probability of obtaining a recovery superior to the better parent.

8-1.1.3 Gamete Selection

Gamete selection is a scheme devised by Stadler (1944) for sampling elite gametes from a population. Stadler's premise was that, if superior zygotes occur with a frequency of p^2 , the superior gametes would occur with a frequency of p . The procedure involves crossing an elite line with a random sample of pollen of plants from a source population; each of the F_1 plants and the elite line are testcrossed to a common tester and the F_1 plants are also selfed; testcrosses are evaluated in replicated trials; and the testcrosses of F_1 plants that exceed the elite line by tester are presumed to have obtained a superior gamete from the source population. Experiments testing the effectiveness of gamete selection reported by Pinnell et al. (1952), Lonnquist and McGill (1954), El-Hifny et al. (1969), and Burton (1982) suggested superior lines could be recovered from the use of gamete selection. But Giesbrecht (1964) reported the method was not effective. It should be emphasized, however, that it is not possible to recover the superior gamete itself because the F_1 plants were self-fertilized; this has been the primary criticism of the purported advantage of the gamete selection scheme (Richey, 1947). The disadvantage of the original concept of gamete selection can be alleviated if individual plants from the source population are crossed to the elite line and also self-fertilized, in which case superior genotypes rather than superior gametes are selected (Hallauer, 1970). Though gamete selection is not used as extensively as pedigree and backcross methods, it does have some intrinsic features that interest breeders, and, consequently, gamete selection is included in some breeding programs.

8-1.1.4 Special Techniques

Several suggestions have been made for the instantaneous derivation of homozygous inbred lines. These techniques have involved the doubling of haploids derived from either maternal or paternal gametes (Chase, 1952; Goodsell, 1961; Kermicle, 1969). Genetic markers were used to identify haploids, and the haploids were doubled to form homozygous diploid inbred lines. The disadvantages of the methods were the low frequency of the occurrence of haploids and doubling of haploids to the diploid state. Kermicle (1969) reported on a spontaneous mutant (*ig*) that increased the frequency of occurrence of haploids (about 3%). Advantages of the use of haploids were the rapid production of new inbred lines and

use in the conversion of inbred lines from normal to sterile cytoplasms. Each of the methods has been used and tested, but it does not seem they are important components of most breeding programs. Although the methods are capable of rapid development of homozygous inbred lines, they would represent a random sample of genotypes that would require the standard methods of evaluation (Thompson, 1954).

Somaclonal variation within inbred lines submitted to tissue culture has been reported (Edallo et al., 1981; McCoy and Phillips, 1982; Earle and Gracen, 1985; Lee et al., 1988). Hence, it seems genetic variation can be derived within inbred lines for selection without making crosses between lines to create genetic variability. Most of the variation observed phenotypically is due to single genes; e.g., albinos. If, however, genetic variation for traits conditioned by 20 or more genes approaches a normal density distribution, tissue culture may permit the recovery of second-cycle lines that include the original genome that also include a gene(s) for other traits; e.g., resistance to a specific herbicide. Tissue culture would have the advantage over other breeding methods for creating variation within an inbred line. The disadvantages, however, would be the same as for the other standard breeding methods: restriction of germ plasm and the probabilities of recovering all the favorable genes of the original line may be low. The genetic changes seem to occur randomly, and, consequently, it would be necessary to evaluate the derived materials similar to other breeding methods (Lee et al., 1988). Somaclonal variation is a recent source of genetic variability that may have an important role in breeding programs. But pedigree and(or) backcross breeding methods will be used to determine its future use.

8-1.1.5 General

After the initial sampling of the landrace cultivars, breeding methods that emphasized inbred line modification have been widely used. A few inbred lines (e.g., B14, B37, C103, and Oh43) possessed traits considered important as lines themselves and in crosses with other elite lines. The lines were included in pedigree and backcrossing breeding programs to modify certain traits (e.g., earlier flowering strains of A632 and CM105 with B14 background and of A619 with Oh43 background), improved pest resistance (e.g., improved first-generation European corn borer resistant strains of B64 and B68 with B14 background and of B76 with B37 background), and improved ear shoot emergence (e.g., Mo17 with C103 background and B76 with B37 background). Because of the nature of the traits under selection, combinations of pedigree and backcross methods sometimes were used to attain the level of expression needed for effective selection. Development of lines B64 and B68 is an example. Both lines were derived from an initial cross of B14 and Amargo 41.2504B made in 1950. B14 was susceptible to first-generation European corn borer leaf feeding, whereas Amargo 41.2504B, an introduction from Argentina,

had first-generation, leaf-feeding resistance. The objective of the cross was to increase the level of resistance to first-generation European corn borer leaf feeding in B14. Two backcrosses were made to B14 to recover the B14 genotype, but with selection for leaf-feeding resistance under artificial infestation. B64 was developed from the second backcross generation (Amargo 41.2504B $\times$ B14³) with the use of standard pedigree selection methods and released in 1964. The level of resistance relative to Amargo 41.2504B, however, decreased with backcrosses to B14. Selfed progenies from the second backcross were artificially infested with corn borer egg masses. Progenies that exhibited higher levels of resistance to leaf feeding were intermated. Selected progenies from the first intermated generation also were infested, rated, and intermated to form the second generation of intermating. Pedigree selection was initiated in the second intermated generation and B68 was released in 1966. Although B64 and B68 were derived from the same backcross generation, the differences in breeding methods used (standard pedigree selection for B64 and intermating, selfing, intermating, and seven generations of selfing for B68) isolated lines with differences large enough to justify release. In addition to the breeding methods used for developing B64 and B68, the source of germplasm also has been a contributing factor in their use (Zuber and Darrah, 1980). Because B64 and B68 also possessed tolerance to corn lethal necrosis, which is caused by a combination of maize dwarf mosaic virus (strain B) and maize chlorotic mottle virus (Doupnik et al., 1981), Amargo 41.2504B also seems to have contributed genes for tolerance to corn lethal necrosis.

The conversion of late-maturity lines to earlier derivatives is another illustration of the effective combination of breeding methods to develop second-cycle lines that have earlier maturity. The methods used to develop earlier maturity derivatives depend on the inbred line being converted and the source of earlier maturity. B14 has acceptable stalk strength, good pest tolerance, rapid grain dry-down, and good combining ability for the central U.S. Corn Belt. Because of these favorable traits, it was considered desirable to obtain earlier maturity second-cycle recoveries of B14 for use at higher latitudes. Earlier maturity recoveries have been obtained, but the breeding methods used have varied. In most instances, early-by-late crosses are produced with subsequent selection for the late phenotype that has earlier maturity. Rinke and Sentz (1961) outlined the breeding methods used in Minnesota. Their program was successful for developing earlier maturity recoveries of genotypes that have been widely used in commercial hybrids (Table 8-2). A632 and A634 were obtained from a cross of Mt42 $\times$ B14. A632 was extracted by pedigree selection after the third backcross to B14. A634 also included three backcrosses to B14, but there was one generation of selfing after the first backcross; there were two additional backcrosses made to B14 after one generation of selfing. A635, A640, and A641 were selected from a cross of ND203 $\times$ B14; A635 was selected after two backcrosses to B14, whereas A640 and

Table 8-2. Breeding methods used in the development of earlier maturity lines from early $\times$ late crosses. Adapted from Rinke and Sentz (1961).

Breeding method after cross No. of generations			
Backcrosses to late parent	Self- fertilization	Frequency of late parent	Example of method
	no.		
4	3	5	A671
3	4	4	A632, A634
2	5	3	A635
1	6	2	A619, CM105†
0	7	1	A640, A641

† CM105 developed by John Giesbrecht (1974, personal communication).

A641 were pedigree selected directly from the F₂ generation. Although Mt42 and ND203 have similar flowering dates (about 85 d), selection for earlier flowering progenies with genotypes similar to B14 must have been easier in crosses to ND203 than to Mt42. In a separate program, CM105 was developed by pedigree selection in the first backcross generation of the cross, CMV3 $\times$ B14 (J. Giesbrecht, 1974, personal communication). Hence, earlier derivatives of B14 were obtained after three (A632 and A632), two (A635), one (CM105), or zero (A640 and A641) backcrosses followed by pedigree selection. The combination of breeding methods depends on the heritability of the trait, expressivity of the trait from the nonrecurrent parent in the cross, and the extent one wishes to recover the phenotype of the recurrent parent. Table 8-3 illustrates briefly some of the methods suggested for managing late $\times$ early crosses. Similar methods could be used for other traits.

The traditional pedigree selection methods of corn breeding obviously have been effective (Duvick, 1977; Russell, 1974, 1984, 1986). But there has been concern that the genetic base of the germ plasm included in breeding programs has become restricted to a few elite genotypes (Anonymous, 1972, p. 97-118). Jenkins (1978) emphasized that the intercrossing of elite lines and reselection to develop second-cycle lines gradually limits the genetic base of the breeding germ plasm. Second-cycle lines have become the main component of present-day breeding programs, at least for lines released by public agencies. Jenkins (1936) listed 350 lines released by public agencies of which only eight (2%) were second-cycle lines. The trend has increased in subsequent decades, and it is estimated that by 1976 76% of the lines released by public agencies were second-cycle lines. The same trends seem to have occurred in the private sector (Smith, 1988).

Some of the limitations of the pedigree method of breeding were suggested by Bailey and Comstock (1976) and Bailey (1977) in simulation studies. They studied intra-line selection within an F₂ population developed from a pair of inbred lines followed by selection among pure lines.

Table 8-3. Breeding selection methods suggested and used for developing early lines from early by late crosses.

Season	Rinke and Sentz (1961)	Baker†	Troyer†
1	Early × late cross	Early × late cross	Balanced set early × late crosses
2	Produce F ₂ 500 plants	Produce F ₂	Yield test for GCA and SCA Produce F ₂
3	Backcross (BC) earliest F ₂ to late parent	Self earliest F ₂ plants	Self earliest 5 to 10% F ₂ plants
4	Grow 15 BC ear-to-row with 100 plants per progeny. Self or BC 10 early plants in 3 early progeny rows	Self earliest plants in early progenies with late parent phenotype	Sib or BC earliest plants to late parent
5	BC or self BC. Select earliest plants in early progeny rows in each generation.	Self earliest plants in early progenies with late parent phenotype	Grow 800 plants and self or BC to late parent the earliest 5 to 10%
6	BC or self BC. Select earliest plants in early progeny rows in each generation.	Self earliest plants in early progenies with late parent phenotype	Grow 800 plants and self or BC to late parent the earliest 5 to 10%
7	BC or self BC. Select earliest plants in early progeny rows in each generation.	Yield test for GCA	Repeat BC or begin pedigree selection
8	Yield test topcrosses	Backcross best to late parent	Repeat BC or begin pedigree selection
9	Make selections	Backcross best to late parent	Repeat BC or being pedigree selection
10	Make selections	Backcross best to late parent	Repeat BC or being pedigree selection

† Raymond Baker and A.F. Troyer (1982, personal communication).

The objective of their studies was to determine the relative probabilities of accumulating in one derived progeny all of the favorable alleles present in either one of inbred lines used to produce the cross. Chances of success, of course, depended on the parents included in the cross. If one parent of a cross is decidedly better than the other parent, as in the case of B14 compared with Amargo 41.2504B, the chances of obtaining a derivative line superior to the better parent are remote. If the two inbred lines included in the cross differ in alleles for a moderate number of loci (e.g., 25 or more), it is unlikely that all of the favorable alleles would be assembled in one line. The other situation examined included two inbred lines that had equal numbers of loci with favorable alleles; e.g., each line included 15 favorable alleles of the 30 loci heterozygous in the F₁. The probability of obtaining a derivative line from this cross that is homozygous for 16 or more favorable alleles is 0.825, and the probability that a derived line is homozygous for 20 or more favorable alleles is 0.292. Johnson (1980) also concluded from a theoretical study that little or no progress could be expected from pedigree selection unless the parents

were nearly equal in value. The theoretical simulation studies support the general observation that selection is more productive within populations developed from crosses of good lines $\times$ good lines than from crosses of good lines $\times$ poor lines. The latter situation is reserved primarily for transferring specific traits that are not available from crosses of good lines.

Although Jenkins (1978) suggested more attention should be devoted to broadening the genetic base of new breeding germ plasm, practical considerations often limit a breeder's choice of germ plasm. New alleles can be introduced from other sources, but new sources usually do not meet the performance standards of the elite germ plasm currently available. The chances of obtaining lines that exceed the currently available well-evaluated inbred lines are not good. Hence, the tendency is to continue to recycle elite inbred lines that have demonstrated performance in hybrids. Other sources of germ plasm will not be used until they have been developed to be competitive with current germplasm sources.

8-1.2 Developing Inbred Lines

The development of inbred lines by self pollination and the evaluation for hybrid performance is the basic procedure in corn breeding programs of the U.S. Corn Belt and in many other areas where corn breeding is done. Information from research and experience has increased effectiveness of breeding procedures compared to earlier years. Breeders continue to search for better methods that will be more effective in the development and identification of inbred lines that have the genetic potential to contribute superior agronomic performance to hybrids. The breeder seeks the procedure that permits the greatest genetic gain per unit of resource input.

Most applied breeders seem to use similar procedures, with minor variations such as plant densities, number of plants per progeny row, number of self pollinations per row, generation at which to start hybrid testing, etc. Probably there is considerable similarity of germplasm sources used by breeders in different programs. Most breeders use an ear-to-row system with inbreeding and selection for several generations until a line is highly homozygous and homogeneous. Some breeders may use only two or three generations of self pollination with subsequent reproduction by sibmating within progenies. This latter procedure will produce somewhat more vigorous lines that yield more seed and produce more pollen than highly inbred lines, but genetic stability may be a problem. Although the single-seed descent procedure used by breeders of self-pollinated crops is used by few corn breeders, there may be a use for it (Brim, 1966). For example, in winter nurseries where the cost per unit land area is high, single-seed descent may be useful to advance a generation for a large number of lines at the S_1 or S_2 level of inbreeding.

One system of inbred-line development relies on phenotypic selection

among and within ear-to-row progenies for several selfing generations before evaluation for hybrid performance. Selection is performed to isolate lines with resistance to important pests, maturity for certain areas of adaptation, plant canopy type, ear size, and grain quality. These traits have reasonably high heritability estimates and are deemed necessary for hybrid performance. For the first progenies of self pollination, S_1 lines, the additive genetic variance among lines is σ_A^2 , and this becomes $2\sigma_A^2$ when $F = 1$. The within-line genetic variance is maximum in the S_1 generation, but decreases rapidly with self pollination and is zero when $F = 1$. Consequently, phenotypic differences among lines increase with continued self pollination in ear-to-row progenies, but success of selection within a line becomes reduced usually by the S_3 and later generations. Therefore, selection effort should be directed primarily to among progenies and less within progenies as inbreeding continues. Testing for hybrid performance may be delayed to about the fifth generation of selfing when the number of selections should be greatly reduced. This breeding system assumes favorable relationships of plant, grain, and ear traits of inbred lines with combining ability for grain yield; thus, the selected lines should be better for hybrid performance than would a random set of lines from the same source (Jenkins, 1929; Hayes and Johnson, 1939).

A second system of inbred development is based on an evaluation for hybrid performance in the early generations of self pollination; e.g., testcrosses of the S_0 plants or S_1 lines. Genotypes that are identified for above-average hybrid performance in these tests are continued in the selfing and selection nursery. The procedure has been called "early testing," and the assumption is that the combining ability of a line is determined early in its development and will change relatively little in subsequent generations of inbreeding and selection. By early testing, the breeder is able to discard some portion of lines that are inadequate in hybrid performance, thus expending resources on materials that have more promise. Jenkins (1935) proposed the early testing procedure; Sprague (1946), Lonnquist (1950), Russell and Teich (1967), Hallauer and Lopez-Perez (1979), Johnson (1980), and Landi et al. (1983) presented data that support it. Russell and Teich (1967) also found that visual selection of inbred lines in a high plant density was just as effective as the early testing procedure in the identification of lines with above-average hybrid yield performance. The original objective of early testing seems valid because the only purpose is to identify those lines that are relatively good or poor and to emphasize selection for those that have above-average combining ability. Proponents do not claim that one should expect an exact ranking at two different stages of inbreeding.

Probably most breeders use a method that is intermediate between the two systems just described, i.e., first hybrid evaluations are of S_2 or S_3 lines. Bauman (1981) found in his survey that breeders begin evaluations as follows: S_2 , 18%; S_3 , 33%, S_4 , 27%. Consequently, testing for hybrid performance and selfing and selection are being done simulta-

neously. Regardless of the system used, a selected line must be one that can be used profitably in commercial hybrid seed production either as a male or female parent.

Self pollination of individual plants within single-plant progenies grown ear-to-row is the most common procedure used to develop inbred lines. This breeding procedure has two important problems: (i) Vigor of the lines is decreased with inbreeding because of loss of favorable dominant alleles and any heterozygous loci that have overdominant effects. Many lines are so poor in seed yield, pollen production, or some other desired agronomic attribute that they cannot be used in a program to produce single-cross hybrid seed. (ii) Effective selection within the row for plants that have desired agronomic traits becomes minimal in generations beyond S_3 ; frequently, phenotypic uniformity is evident by the S_2 generation. Once the locus becomes homozygous in a line no further selection for segregating types is possible.

A second system that may be used to develop inbred lines involves some method of sibmating rather than self pollination. Stringfield (1974) has called this a conservative procedure, and he has given a theoretical discussion of the advantages of such a method compared with the development of lines by self pollination. Sib-mating permits the recombination and segregation for loci that have more than one allele in the progeny, thus giving the breeder more opportunity to select for desirable attributes. If sib-mating per progeny involves enough plants, inbreeding will be at a slower rate so that the plants are more vigorous than in a highly inbred line. Such lines would be better for seed yield and pollen production and, therefore, fewer such lines would have to be discarded because they couldn't be used in single-cross hybrid seed production. Sib-mated lines would have some level of genetic heterogeneity; thus, crosses of such lines would have less aesthetic value in hybrid appearance, which seems important to many producers. Greater heterogeneity, however, may give greater stability of field performance. Stangland and Russell (1981) reported that the variability within hybrids of $S_2 \times S_2$ lines was similar to hybrids that have related-line crosses for parents, but less variable than double crosses. Such lines may have gene frequency changes over a period of several generations of maintenance. Because of the heterogeneity of loci it may be more difficult to insert some single genes, as for disease resistance, or to convert to male-sterile cytoplasm by a back-cross procedure. Also, it will be more difficult to identify contaminants in lines that are not highly inbred.

An important problem in a conservative program as outlined by Stringfield (1974) is the number of lines that one could develop for evaluation. Considerable time is required to select plants for sib mating at pollination and again at harvest, which means that it is more time-consuming than the standard practice of self pollination. Also, the success is dependent upon the ability of a person to select those plants that have the desired attributes (Mock and Pearce, 1975). Consequently, it is not

a procedure to be used by untrained personnel who do much of the pollination in corn-breeding nurseries.

8-1.3 Correlation of Inbred Traits with Hybrid Performance

Breeders assume favorable correlations between plant, ear, and grain traits of the parental lines and performance in hybrid combination. Several studies have shown that correlation of an inbred trait with the same trait in the hybrid is relatively high, except for yield. Although many r values of inbred traits, including yield, with hybrid yield have been positive and significant, in most instances they have been too low to be of predictive value. Consequently, extensive evaluation in hybrid progenies is required to determine the true value of an inbred.

The earlier correlation studies (Jenkins, 1929; Hayes and Johnson, 1939) were done in field husbandry conditions that were at a much lower productivity index than those now used in corn production. The relationship between inbred traits and hybrid performance, however, may be greater in a higher productivity environment with the improved cultivars.

Results from two breeding methods studies (Russell and Teich, 1967; El-Lakany and Russell, 1971) suggested that greater relationships may occur when materials are grown in stress environments, such as high plant densities. Data were presented by Russell and Machado (1978) on inbred lines and correlations of inbred-line traits with hybrid yields when materials were grown at different densities. The source population was BS1 synthetic, which is genetically diverse and adapted to the U.S. Corn Belt. After four generations of phenotypic selection and self pollination, S_1 to S_4 , they had 76 S_5 lines. The lines were evaluated in relatively low and high plant densities and testcrosses of the lines (double-cross hybrid tester) were evaluated in low, intermediate, and high plant densities. Although the lines had been selected rigorously for several agronomic traits, there were highly significant differences among the lines for 13 agronomic traits. Also, there were highly significant differences among the lines for testcross yield performance. None of the plant traits in either density of the inbreds had correlations with hybrid yields that were high enough to be of predictive value. Only leaf area showed an important relationship, and it was greater for the lower density than for the higher density of the inbreds, and increased from the highest to the lowest density of the testcrosses. For ear and grain traits, except grain yield, r values were slightly greater at the higher inbred density, but changed little from the lowest to the highest density of the testcrosses. For inbred grain yield, r values were greater at the higher inbred density, but changed little from the lowest to the highest density of the testcrosses. For example, inbred yields at the low density correlated with testcross yields at low, intermediate, and high densities had r values of 0.33, 0.28, and 0.33; for inbreds at the high density and testcross yields at low, intermediate, and

Table 8-4. Multiple correlation coefficients between traits of inbred parents at two densities and hybrid yields at three densities. Adapted from Russell and Machado (1978).

Traits correlated	Hybrid densities			
	Low	Medium	High	Avg.
Hybrid yield vs.				
all inbred traits	0.54	0.52	0.54	0.56
inbred plant traits	0.43	0.38	0.30	0.38
inbred ear and grain traits	0.42	0.42	0.51	0.49
Hybrid yield vs.				
all inbred traits	0.61	0.60	0.64	0.65
inbred plant traits	0.46	0.35	0.36	0.40
inbred ear and grain traits	0.53	0.53	0.60	0.60

high densities the r values were 0.42, 0.40, and 0.43, respectively. The r values for the inbreds at high density with testcross yields were higher than obtained in most earlier studies. Selection for high-yielding inbreds would tend to select lines that are above average for hybrid yields. Lamkey and Hallauer's (1986) data support this conclusion.

Actually, the corn breeder selects for total phenotype, or an ideotype, of the inbred line; consequently, it seems more appropriate to consider multiple correlation coefficients (Table 8-4). The R values were greater for the higher density of the inbred lines than for the lower density; plant traits showed decreases from the highest to the lowest density of the testcrosses, whereas ear and grain traits showed increases from the lowest to the highest density of the testcrosses. The R values suggest that visual selection for inbred development in a higher plant density should be more effective for hybrid yield performance. For the higher density of the inbreds and highest density of the testcrosses, $R^2 = 0.41$, which indicates that 41% of the variability of the testcrosses for yield was accounted for by the variability among inbred lines for 13 plant, ear, and grain traits. Furthermore, the selected lines would be much better than a random set from the same source for traits such as maturity, height, pest resistance, grain quality, and seed yield.

The r values obtained by Russell and Machado (1978) may have been confounded by the inbred selection that would have reduced genetic variability. Gama and Hallauer (1977), however, used random lines from 'Iowa Stiff Stalk Synthetic' (BSSS) and obtained R values for inbred traits with hybrid yields of only 0.23 and 0.21 for two methods of calculation. They concluded that phenotypic appearance of a line does not seem a good indicator of its worth in single-cross hybrids.

Some evidence for a stronger relation of inbred yield and yield components with hybrid yields is evident in Tables 8-5 and 8-6 (Russell and Machado, 1978). Data in Table 8-5 are for the five highest and five lowest yielding testcrosses in the highest density. The high group had only an average decrease of 0.11 Mg ha⁻¹ across densities, whereas the low group

Table 8-5. Grain yields and percentage of barren plants for the five highest- and five lowest-yielding testcrosses, averaged for eight environments. Adapted from Russell and Machado (1978).

Selection no.	Plants ha ⁻¹ (× 1000)			Avg.	Barren plants†
	39.0	54.0	69.0		
	Mg ha ⁻¹				%
4	6.86	6.42	6.77	6.69	18.6
34	7.17	6.74	6.92	6.94	10.4
53	7.53	6.94	6.76	7.08	6.8
54	6.56	6.91	6.80	6.76	11.4
55	6.76	7.36	7.06	7.06	9.8
$\bar{x}$	6.97	6.87	6.86	6.91	11.4
18	6.10	5.67	5.04	5.60	20.3
27	5.70	5.66	4.97	5.44	30.6
39	6.02	5.59	4.94	5.52	15.6
63	6.21	5.48	5.24	5.60	34.6
65	5.68	5.50	5.08	5.42	28.0
$\bar{x}$	5.94	5.58	5.05	5.52	25.8

† At 69 000 plants ha⁻¹.

Table 8-6. Ear and grain data in the high density for the inbreds per se that were the five highest and five lowest in testcross yield performance. Adapted from Russell and Machado (1978).

Selection no.	Ear length	Wt. 300 kernels ⁻¹	Yield
	cm	g	Mg ha ⁻¹
4	12.8	73.5	4.58
34	17.2	71.2	6.02
53	13.2	56.0	3.40
54	12.6	76.5	3.62
55	15.4	79.4	6.60
$\bar{x}$	14.2	71.3	4.84
18	12.0	68.6	3.21
27	6.8	55.0	1.98
39	11.4	56.2	3.12
63	8.8	71.4	2.23
65	11.6	71.8	2.98
$\bar{x}$	10.1	64.6	2.70

had a decrease of 0.89 Mg ha⁻¹. The low group had a significantly higher frequency of barren plants. For the parental lines at the high density, the average yield for the high group was 2.14 Mg ha⁻¹ more than for the low group (Table 8-6). Ear length and weight per 300 kernels were important components in the yield differences.

A stress environment may be caused by a low availability of N. Balko and Russell (1980b) evaluated 40 inbred lines from BSSS and 20 single crosses of these at five N levels: 0, 60, 120, 180, and 240 kg of N ha⁻¹ in four location-year environments. Inbred line plant, ear, and grain traits had little relationship with single-cross yield at any N level; only two significant *r* values were obtained. Gama and Hallauer (1977) also found

Table 8-7. Multiple correlations coefficients between the traits of 40 inbred parents and the yield of 20 single crosses, calculated at each N level and combined over all N levels. Adapted from Balko and Russell (1980).

Traits correlated	Nitrogen applied, kg ha ⁻¹					Com- bined
	0	60	120	180	240	
Hybrid yield vs.						
all inbred traits	0.94	0.80	0.72	0.70	0.88	0.76
inbred plant traits	0.87	0.71	0.57	0.41	0.51	0.73
inbred ear and grain traits	0.42	0.28	0.40	0.47	0.69	0.52

low *r* values when using inbred lines from this source. Multiple *R* values between 13 inbred traits and single-cross yields are presented in Table 8-7. With all inbred traits, the highest *R* values were from N levels of 0 and 240 kg ha⁻¹. For plant traits, *R* increased from the 180 kg of N level to the zero level, but for ear and grain traits *R* increased from the 60 kg of N level to the 240 kg of N level. Yield response to N levels (Balko and Russell, 1980a) suggested that the most efficient single crosses for N use may be identified best when grown in a soil environment where available N is equivalent to 120 kg of N ha⁻¹.

8-1.4 Testers and Testing

Usually it is relatively simple to develop a large number of inbred lines that are agronomically satisfactory as lines per se. The primary problem is to have adequate testing of the lines to determine performance in hybrid combination. The most complete information for hybrid performance is obtained in a single-cross diallel because this procedure gives information of general and specific combining ability (Sprague and Tatum, 1942). The single-cross diallel is not practical, however, because of the large number of crosses required for only a few lines. Generally, for preliminary hybrid evaluation the breeder needs to determine the relative general combining ability for new lines.

Davis (1927) and Jenkins and Brunson (1932) suggested use of a common tester to evaluate lines for general combining ability. In earlier years, breeders used an open-pollinated cultivar as the common tester, and it would be highly heterogeneous. Matzinger (1953) showed that a heterogeneous tester contributes less to line × tester interaction than does a narrow genetic-base tester. It was suggested that a double-double cross tester that included the eight most commonly used lines within a given maturity group would be a good tester for general combining ability.

The choice of a tester is an important decision. Hull (1945) concluded, on a theoretical basis, that the most efficient tester would be one that is homozygous recessive at all loci. Rawlings and Thompson (1962) stated two requisites for a good tester to evaluate inbred lines: (i) the entries under test must be classified correctly; and (ii) the tester must discriminate effectively among the materials under test. Hallauer (1975) suggested that

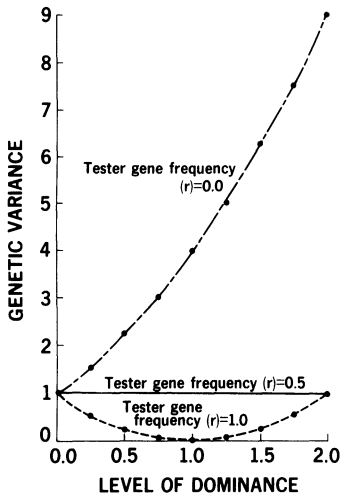


Fig. 8-3. Relation of total genetic variation to tester gene frequency and level of dominance. Adapted from Rawlings and Thompson (1962).

a tester should include simplicity in use, provide information that correctly classifies merit of lines, and maximizes genetic gain. Rawlings and Thompson (1962) showed that, for a given set of testcrosses, the genetic variation among the testcross progenies was directly proportional to the square of $[1 + (1 - 2r_i)a_i]$, where r_i is the allele frequency at the i th locus for the tester and a_i is a measure of dominance at the i th locus. Thus, genetic theory indicates that the best tester is one that has low allele frequencies for the favorable alleles that condition agronomic traits in the materials being evaluated (Fig. 8-3; Hallauer, 1975). All testers will give an equal measure of genetic variance if there is no dominance. As the level of dominance increases, however, the advantage of a tester with low allele frequency is obvious.

Rawlings and Thompson (1962) examined the tester theory by an evaluation of crosses in which the parental materials had been classified for level of performance in previous studies. Their results supported the theory that low-performing testers, which they assumed to have a low frequency of favorable alleles at the important loci, were the most effective testers. Further information comparing types of testers was obtained in a detailed study by Hallauer and Lopez-Perez (1979). They used an unselected sample of 50 S_1 and 50 S_8 inbred lines whose source was BSSS. The 50 S_8 lines were direct descendants of the 50 S_1 lines. The lines were crossed to five testers: (i) BSSS, the parental source population; (ii) BS13(S)C1, which is a BSSS population after eight cycles of recurrent selection, primarily for grain yield; (iii) BSSS-222, a low-yielding S_8 line derived from BSSS; (iv) B73, a high-performance inbred line derived from BS13(HT)C5 after five cycles half-sib recurrent selection; and (v) Mo17, an unrelated high performance line. Frequencies for favorable alleles in the four testers related to the tested lines would be expected to be highest for B73, followed in descending order by BS13(S)C1, BSSS, and BSSS-

222. Inbred Mo17 is unrelated to the other testers and, therefore, would be expected to differ in frequencies of favorable alleles from the other testers. The relative magnitudes among testers for the estimated components of variance when S_1 lines were evaluated are as expected on the basis of gene frequencies (Table 8-8). For the S_8 lines, the estimated components of variance are greater than for the S_1 lines, as would be expected, and the relative magnitudes for the related testers are similar to the S_1 lines, except for B73 which is larger.

The testers used by breeders will be dictated by the stage of development of breeding programs, availability of testers, type of material under test, and type of hybrids for which the lines are to be used. Probably in established corn-breeding programs, the first use of any new inbred lines will be with one or more lines that are already established as parental lines. Thus, it seems logical that, for the first or preliminary evaluations of new lines for hybrid performance, one or more of the established lines should be used as testers, either individually or in some type of cross. If specific combining ability is an important factor, the breeder will be taking advantage of it when the testers are individual lines. For lines that are identified as worthy of advanced testing, additional proven lines in the maturity group can be used as testers. The philosophy for choice of tester in earlier years was that a heterogeneous cultivar (i.e., open-pollinated cultivar) was needed if the purpose was to obtain a measure of general combining ability. The use of a narrow genetic-base tester, such as an inbred line or a single-cross hybrid, would emphasize specific combining ability. Results from more recent studies (Horner et al., 1973, 1976; Russell et al., 1973; Hoegemeyer and Hallauer, 1976; Russell and Eberhart, 1975; Walejko and Russell, 1977) show that an inbred line tester gives relatively more information for general than for specific combining ability. Bauman's (1981) survey of corn breeders in the USA found that 89% use an inbred line and 11% use a single cross.

Table 8-8. Estimates of components of variance and standard errors for yield ($Mg\ ha^{-1}$) for S_1 and S_8 testcrosses. Adapted from Hallauer and Lopez-Perez (1979).

Tester†	S_1	S_8
BSSSCO	0.184 ± 0.065	0.417 ± 0.120
BS13(S)C1	0.106 ± 0.045	0.341 ± 0.102
BSSS-222	0.217 ± 0.064	0.387 ± 0.111
B73	0.038 ± 0.035	0.264 ± 0.080
Mo17	0.259 ± 0.085	0.298 ± 0.095
Avg.	0.161 ± 0.059	0.341 ± 0.102

† BSSSCO is the original Stiff Stalk Synthetic population from which the lines under test were developed by single-seed descent. BS13(S)C1 is an improved strain of BSSSCO after seven cycles of half-sib selection with double-cross Ia13 as tester and one cycle of S_1 - S_2 selection. BSSS-222 is an inbred line derived from BSSSCO and identified as one of the lowest-yielding lines. B73 was derived from BS13(HT)C5, which is a strain of BSSSCO after five cycles of half-sib selection. Mo17 was obtained by pedigree selection from the cross of (187-2 × C103) and was considered unrelated to the other materials included for test.

Single-cross hybrids have become the predominant type in the USA and in many other areas of corn production. Because vigorous parental lines are required, greater attention is given to seed yield and pollen production than was necessary when double crosses were used. Consequently, yield testing of the lines per se along with hybrid evaluation may be justified. It probably should not be necessary to test the lines as extensively as testcrosses. A single observation row in the breeding nursery with open pollination can give a good indication of potential seed production and, if grown for 2 to 3 yr while the line is being evaluated for hybrid performance, may be adequate to determine if the line can be used in seed production. Testing of the lines per se may give information that can be used to predict hybrid performance, except for grain yield. Hallauer and Lopez-Perez (1979) obtained no significant r values for yield between the lines per se and their testcrosses. Jensen et al. (1983) found for yield that topcrosses of S_2 lines (S_2 TC) were a much better predictor of topcrosses of S_5 line (S_5 TC) performance than were S_2 's per se. Only two of six experiments showed r values significant ($P \leq 0.05$) for S_2 vs. S_5 TC, compared with six of six experiments for S_2 TC vs. S_5 TC. Smith (1986) used a computer simulation procedure to calculate correlations between lines per se and testcross performance, and testers were of three types: average, above average, and unrelated. The r values between lines per se and the three testers were 0.34, 0.22, and 0.28, respectively. These simulation results support actual data that yields of lines per se are not good predictors for the lines in hybrids.

The generation of inbreeding in which breeders begin evaluation for hybrid performance seems to depend on personal choice. A philosophy of early testing is that selection for two to three generations before hybrid testing is not effective in enhancing combining ability, whereas breeders who delay hybrid testing until the S_4 or a later generation believe selection will obtain lines that are better than average. The source population may also be a decisive factor. If the source population is elite material because of considerable earlier improvement, further selection during generations of self pollination may not achieve further gains, and hybrid testing can be started in early generations. Conversely, if the source population is relatively unselected material, visual selection during two or three selfing generations is useful to select for certain agronomic traits, and hybrid evaluation may be delayed to about S_4 . Opponents of the early testing procedure believe the system does not justify the additional cost and cite low r values between early and late generation tests to support their argument.

8-1.5 Breeding Sources

Planned crosses of inbred lines are the most frequently used sources in which to begin the isolation of inbred lines (Bauman, 1981). Single-cross hybrids are used most frequently. Most backcross sources will have

only one backcross to the recurrent parent, except in instances where the purpose is to transfer one or two genes that control a specific trait. Dudley (1982) showed that, in most instances, it would not be desirable to use more than one backcross. Strict attention should be given to maintaining known heterotic patterns when planned crosses are used. Breeders also use competitive private company hybrids as source material, but, in such instances, usually it will not be known where derived lines fit in a heterotic pattern.

The selection of the breeding source material is an item of prime importance. Pedigree selection in planned crosses permits the use of high-combining lines, but has some limitations such as decreasing genetic diversity and, perhaps, the failure to introduce new, favorable alleles into the program. Frequently, the breeder's goal is to improve one or both parent lines of an elite single cross. Dudley (1984a, b) has presented a method, along with the theory and some supporting data, that should be helpful to assist a breeder in the selection of donor lines.

Limited use is being made of synthetic cultivars (Bauman, 1981). The selection of a synthetic may be based on the pedigree of the synthetic and on information from previous evaluations. The diallel analysis and evaluation of synthetics per se are useful to identify superior sources (Hallauer, 1972; Hallauer and Eberhart, 1966; Hallauer and Sears, 1968; Hallauer and Malithano, 1976; Lamkey and Hallauer, 1984). Improved versions of a synthetic are expected to be better sources than the original synthetic (Russell, 1985b). Dudley (1984c; 1988) has presented a method for identifying populations of exotic germ plasm that contain useful new alleles.

A part of sampling in inbred development is the number of sister lines to grow from each S_1 line or from individual lines in later generations. Greater gain is expected from sampling among S_0 -derived lines rather than within lines at the S_1 and later selfed generations. Proliferation of sister lines from individual S_1 lines, or from individual lines in later generations, should be avoided because it is not an efficient use of resources.

8-1.6 Types of Hybrids

Basically, three types of crosses have been used commercially: double crosses, three-way crosses, and single crosses. Delay in the widespread use of single crosses probably occurred because published data indicated greater genotype $\times$ environment interaction, or less performance stability, for single crosses than for double crosses. Data published by Sprague and Federer (1951) indicated an average situation, but it did not mean there were no single crosses equal to the best double crosses for stability of performance. The three-way cross has a single cross as female parent and an inbred line as male parent. Thus, the seed is produced on a high-yielding parent, but the male parent is an inbred line that may not always

be a reliable pollen producer, which has probably been a restriction for the use of three-way crosses. The related-line single cross is another hybrid type that has been widely used. In this instance one or both parents are crosses of related lines, thus the parents are more vigorous than pure-line inbreds. There is no standard definition for related lines and, in some instances, the term has been used loosely; e.g., designating two lines from the same source synthetic as related lines. More generally, for two lines to be designated as related, the genetic commonality would be 50% or greater. Single-crosses became more widely used in the 1960s in some areas, whereas double-cross hybrids are still the predominant type in some areas where seed production for single crosses is a risky adventure because of unfavorable climatic conditions.

Each of the three basic hybrid types has advantages and disadvantages. Theoretically, double crosses are expected to be more stable than single crosses over a series of environments because they are genetically heterogeneous. This has been designated as genetic homeostasis by Lerner (1958) or population buffering by Allard and Bradshaw (1964). Several studies have confirmed this comparison, but some individual single crosses may be as stable as the most stable double cross (Eberhart and Russell, 1966). Such single crosses may have developmental homeostasis (Lerner, 1958) or individual buffering (Allard and Bradshaw, 1964).

On the basis of simple gene action (i.e., additive and dominance but no epistasis), single crosses are expected to be superior to double crosses. Eberhart and Russell (1969) compared 45 single crosses among 10 elite inbred lines with a balanced set of 45 double crosses for the same lines in 22 environments in the U.S. Corn Belt. Averaged over all hybrids, the single crosses yielded 1.9% more than the double crosses, but the highest-yielding single cross yielded 8.0% more than the highest-yielding double cross. For yield, the double crosses had less genotype $\times$ environment interaction than the single crosses; however, 2 of the 10 highest-yielding single crosses were as stable as the most stable double crosses. Because the single cross has only two parental inbred lines, one should expect to identify certain single crosses that are superior to double crosses for other agronomic traits such as root and stalk strength, pest resistance, and grain quality.

The expected relative performance of single crosses $>$ three-way crosses $>$ double crosses may be changed by some types of epistatic gene action. Epistatic gene action has been observed in several studies (Bauman, 1959; Gorsline, 1961; Sprague et al., 1962; Sprague and Thomas, 1967; Weatherspoon, 1970; Stuber et al., 1973; Schnell and Singh, 1978; Melchinger et al., 1986). The effects of epistasis may be negative or positive, i.e., the yield of a three-way cross hybrid may be either greater or lesser than predicted from the mean of the two nonparental single crosses. In 60 comparisons for yields of the three-way crosses with predictions from component single crosses, Sprague et al. (1962) obtained significant epistasis and for all, except one, the three-way cross yielded less than

predicted. Schnell and Singh (1978) reported that 9 of 36 comparisons were significant, and in all instances the single-cross prediction was greater than observed for the three-way crosses. Stuber et al. (1973) also found evidence for epistasis, but they concluded that the effects of genotype $\times$ environment interaction were of greater importance than epistasis.

8-1.7 Maintenance of Inbred Lines

A primary purpose for developing lines that are highly inbred is to obtain genotypes whose genetic integrity will be maintained without change during generations of reproduction. At least two assumptions are involved: (i) the inbred line is homozygous and, therefore, no further changes can occur because of heterozygous loci that have persisted from the S_0 plant; and (ii) there are no mutations that give rise to genetic changes. Several studies have shown that neither of these assumptions is valid. Sprague et al. (1960) studied the genetic stability of 11 inbred lines, in which each line evolved from a doubled monoploid plant. Such lines would be truly homozygous in the first diploid generation. They found, however, that these lines became genetically variable with successive generations of reproduction by self pollination, and calculated that there were 4.5 mutations per attribute per 100 gametes tested. A similar study that used inbred lines developed by the conventional system of self pollination in ear-to-row progenies found a mutation rate of 2.8 per attribute per 100 gametes tested (Russell et al., 1963). Busch and Russell (1964) found 38% of the changes in two lines were expressed in hybrid progenies.

Relic heterozygosity either from the original S_0 plant or from a mutation in some later generation may also be the cause for measurable changes over generations of reproduction. This has been shown to occur in lines after they have been interchanged among experiment stations and then reproduced in different environments for several generations. Fleming et al. (1964) observed significant variation among stocks in all but one of six inbred lines that had been maintained at five to seven experiment stations, and concluded that, because of selection, variants were isolated that had become adapted to their particular environment. Subsequently, Fleming (1971) found that more than 50% of the significant variations among strains were detected as significant in testcrosses. Grogan and Francis (1972) found significant variation for one or more traits in four of six inbred lines obtained from six experiment stations. They also observed an unexpected amount of heterosis among source $\times$ source crosses of the same line.

The genetic stability of an inbred line that is maintained for a number of years at one location is important to breeders and seedsmen. Russell and Vega (1973) reported a study in which 11 long-time inbred lines were maintained for 11 successive generations with self pollination in ear-to-row progenies. They measured 10 quantitatively inherited plant, ear, and grain traits and found for 106 tests of differences among generations that

42 were significant. The evidence indicates that changes occurred because of both mutations and segregation from residual heterozygosity. In a similar study, Bogenschütz and Russell (1986) evaluated genetic stability in 10 long-time inbred lines that were maintained for 11 successive generations by both self pollination and sib mating. There were 93 possible comparisons to check for genetic stability in each method of maintenance, and 28 in the sib mating and 52 in the self pollination showed significance among generations. Also, over all generations, means of the two methods were different for 51% of the comparisons, and the selfed lines were less vigorous for 79% of the significant comparisons. They concluded that sib mating lessens the observed effects of genetic instability. In both these previous studies, some lines seemed inherently stable and others seemed inherently unstable. Fleming and Kozelnicky (1965) also compared sib mating with self pollination and reported a yield trend in favor of sib mating.

Breeders and seedsmen will use a system of line maintenance that seems most logical for a given situation. A system of self pollination with progenies grown ear-to-row for breeders' seed offers the best opportunity to observe changes for plant, ear, and grain traits. A large number of ear-row progenies per line is probably unnecessary because genetic changes usually are not found unless measurements are made in several replications. Reproduction by either sib mating or self pollination will gradually increase genetic variability. Changes that occur usually are small in effect and probably not of practical importance in most instances. If, however, a line is reproduced over a period of years—some lines may remain in a program for up to 20 yr—accumulation of changes may gradually give rise to a line that is considerably different from the line as it was in the S_6 generation. A stock culture of a line should be placed in cold storage, with reproduction only as needed to maintain seed viability, so that the breeder or seedsmen can return to this culture at any time. The time at which the culture is placed in storage will vary among stations, but a logical time seems to be when the line is released from an experiment station or when it is first used for commercial seed production.

8-2 IMPROVEMENT OF GERM PLASM

8-2.1 Introduction

The pure-line concept suggested by Shull (1909, 1910) was extensively applied and proved useful for the development of inbred lines and hybrids. It became evident, however, that other germplasm sources were needed to develop new, improved lines. The first logical sequel was the recycling of the superior lines via use of pedigree and backcross breeding methods. Because of the nature of the traits under selection and the need to develop improved sources of germ plasm, it was realized different

selection methods were needed to supplement the classical pedigree and backcross breeding methods.

Many of the traits considered important in corn breeding have a complex inheritance and, consequently, are not easily amenable to visual selection among a limited number of individual plants. These types of traits are designated as quantitative traits; i.e., the traits are controlled by a relatively large, unknown number of genetic factors with each factor having a small effect on the expression of the trait. Additionally, the effects of the individual factors are affected by the environments in which they are measured. The distribution of the phenotypes, based on the genetic and environmental effects, is usually assumed to approximate a normal density distribution (Fig. 8-4). Because of the complexity of the inheritance of many of the traits considered important in corn breeding, it was not possible to accurately measure the genetic merit of individuals based on visual selection. Hence, the original suggestions of mass selection and ear-to-row selection were not effective for the improvement of yield (Fig. 8-2). It was acknowledged, however, that the genetic factors involved in the inheritance of quantitative traits behaved in a Mendelian manner, but it was not possible to correctly classify individuals into discrete classes. The problems related to the improvement of traits inherited in a quantitative manner included the genetic basis of quantitative traits, methods of measuring differences among individuals, and methods of selection to improve the traits of interest. These problems were being addressed during the 1930s and 1940s to further exploit Shull's inbred-hybrid concept.

Three factors had a significant impact in the rationale used for the improvement of corn germ plasm: development of quantitative genetic theory and its application to plant populations; further developments in experimental and mating designs and data analysis; and development of selection procedures to increase the frequency of favorable alleles of com-

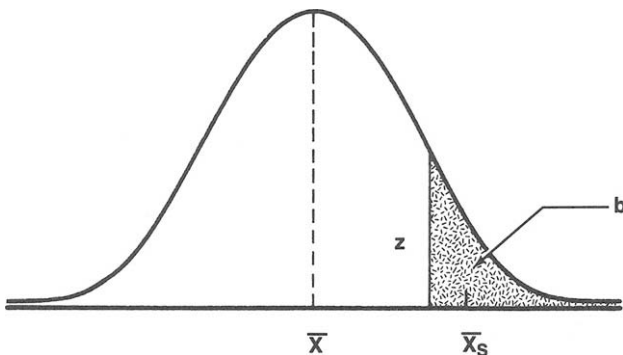


Fig. 8-4. Phenotypic distribution of a quantitative trait in a hypothetical population showing the population mean ($\bar{x}$), portion (b) selected for recombination, height or ordinate (Z) at point of tuncation selection, and the mean ($\bar{x}_s$) of the selected progenies used in recombination.

plex traits. Each of the three factors supported the others. It was realized that information on the nature of the inheritance of quantitative traits was necessary for selection to be effective. Proper experimental designs (both field and mating) were needed to obtain valid estimates and to permit the interpretation of the data (Dudley and Moll, 1969). Empirical studies suggested genetic variability within corn populations, particularly the portion due to additive genetic effects, was adequate and should not be a serious constraint in the improvement of corn populations (Hallauer and Miranda, 1981). Selection methods were developed to capitalize on the information obtained from the quantitative genetic studies. A valid basis, therefore, was established to improve germ plasm to meet specified objectives.

The newer techniques and information were accepted and applied in corn breeding. Because of corn morphology and mode of reproduction, most of the suggestions were applicable and could be tested for the improvement of corn populations (Hallauer and Miranda, 1981). Based on the information reported and their interpretations, selection schemes were developed for the improvement of quantitative traits to generate improved sources of germ plasm. These selection schemes are generally referred to as recurrent selection.

8-2.2 Recurrent Selection—Methods

As the name implies, recurrent selection includes selection methods that are conducted in a repetitive manner (Fig. 8-5). Regardless of the trait under selection, the objectives of recurrent selection are twofold: (i) increase the frequency of the favorable alleles, which is to change the mean of the population in a favorable direction; and (ii) maintain genetic variability for continued selection by intermating superior progenies for

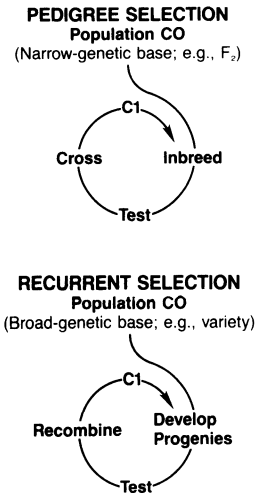


Fig. 8-5. Cyclical nature of pedigree and recurrent selection for the systematic improvement of corn germ plasm.

each cycle of selection. In its broadest context, the pedigree breeding methods that include crossing of elite lines to select second-cycle lines are a form of recurrent selection (Fig. 8-5); i.e., elite lines are crossed to initiate pedigree selection in either F_2 or backcross populations. Usually, recurrent selection is reserved for selection conducted repetitively for quantitative traits in genetically broad based populations.

To realize the objectives of recurrent selection, three distinctive phases are common for all except phenotypic mass selection: (i) development of progenies from the selected source populations; (ii) evaluation of progenies in replicated trials that may be conducted in different environments; and (iii) recombination of selected progenies, based on the evaluation trials, to form a population for continued selection (Fig. 8-5). The three phases complete one cycle of recurrent selection. The types of progenies developed and evaluated, the extent of evaluation, the methods of recombination, and the number of growing seasons or years required to complete one cycle of recurrent selection varies among recurrent selection methods. Thus, careful consideration must be given to each of these variables to maximize genetic gain on either a per cycle or a per year basis (Eberhart, 1970; Hallauer, 1985).

Decisions that are critical to the ultimate success and usefulness of germ plasm improved via recurrent selection need to be considered (Eberhart, 1970; Hallauer and Miranda, 1981; Hallauer, 1985). Decisions are required for choice of population(s) in which to initiate selection, types of progenies evaluated, extent of evaluation, effective population size, method of recombination of selected progenies, and efficient use of growing seasons for each phase of the program. For some items, information and data are available to provide guidelines in making choices. For others, only limited data are available to support a particular choice of alternatives. Choice of germ plasm for use in selection is important to meet the objectives of selection, but critical information to base the decision on choice of germ plasm is often limited. If proper choices were made for all other aspects of the recurrent selection program, the ultimate success of selection may be disappointing because the favorable alleles either were not present or were at low frequencies.

Relative progress within a chosen source of germ plasm also will be influenced with the use of an "effective screen" to measure genetic differences among progenies. Depending on the trait under selection, determination of the genetic differences among progenies will depend on the screening techniques and resources available. Effective screens, for example, have been developed for the artificial infestation and infection for many of the common pests of corn, analyses for the chemical composition of the plant and grain, and measures for determining maturity. Selection, therefore, is effective where the genetic differences can be measured accurately. Penny et al. (1967) reported that three cycles of selection for leaf-feeding resistance to the first-generation European corn borer were adequate to develop germplasm sources with acceptable levels of resis-

tance. Manual application of laboratory reared egg masses on S_1 progenies was effective in determining the genetic resistance of S_1 progenies to leaf feeding and minimizing escapes. Williams and Davis (1983) infested individual corn plants with southwestern corn borer [*Diatraea grandiosella* (Dyar)] egg masses and were not successful to increase the level of resistance after two cycles of individual plant selection. Although artificial means of infestation were used, Williams and Davis (1983) concluded that some type of progeny evaluation rather than individual plant selection was needed for selection to be effective.

Grain yield is the most important economic trait in corn breeding. Hence, response, whether direct or indirect, of yield to selection is usually of prime importance. Yield is a complex trait whose expression is dependent on the environmental effects experienced during the life of the individual plants and progenies. Effective screens for determining genetic differences for yield among genotypes have been limited because of the sporadic and unpredictable environmental effects. Also, the measures of genetic differences will depend on the types of progenies evaluated (Lamkey and Hallauer, 1987). The heritabilities of grain yield can vary from $< 10\%$ for individual plants in one environment to $> 80\%$ for S_2 progenies evaluated in two replications at three environments (Table 8–9). Thus, types of progenies used can have an effect on the relative ability for determining differences among genotypes, and, therefore, effectiveness of selection. Replicated trials in a series of environments (location-year) are routinely conducted to separate the environmental and genetic effects. But the effectiveness of selection also is dependent on the types of progenies evaluated.

Recurrent selection methods are not new. Sprague and Brimhall (1950) credit Hayes and Garber (1919) with the first use of the objectives of recurrent selection to develop cultivars with greater protein content. Only one cycle of selection and recombination, however, was completed. It

Table 8–9. Pooled estimates of six parameters of grain yield for seven recurrent selection methods. Adapted from Lamkey and Hallauer (1987).

Method of selection	Parameters†					
	σ^2	σ^2_{GE}	σ^2_G	σ^2_P	h^2	GCV
	Mg ha ⁻¹ × 10 ²					
Half-sib	78.1 ± 3.3	9.2 ± 3.0	22.7 ± 2.9	38.8 ± 2.8	58.5	7.5
Broad-base tester	55.1 ± 0.6	9.9 ± 0.6	21.0 ± 0.7	33.5 ± 0.7	62.7	6.9
Inbred tester	79.1 ± 1.3	9.6 ± 1.1	19.0 ± 1.0	35.4 ± 0.9	53.8	5.9
Full-sib	90.0 ± 2.7	18.1 ± 2.8	44.3 ± 3.2	65.1 ± 3.1	68.0	11.0
S_1	53.3 ± 1.0	14.2 ± 1.0	54.0 ± 1.9	67.6 ± 1.9	79.8	18.4
S_2	54.5 ± 1.0	24.1 ± 1.3	58.5 ± 2.2	75.6 ± 2.2	77.3	24.3
Reciprocal full-sib	107.2 ± 2.4	13.8 ± 2.2	27.3 ± 1.9	49.8 ± 1.8	54.9	7.7

† σ^2 , σ^2_{GE} , σ^2_G , and σ^2_P = estimates of experimental error, genotype × environment interaction, genotypic, and phenotypic components of variance, respectively. h^2 = estimate of heritability on a progeny mean basis. GCV = genetic coefficient of variation.

seems Jenkins (1940) was the first to appreciate the long-term effects and the application of recurrent selection principles in corn breeding. Jenkins (1940) provided a detailed description of a method that included development of S_1 progenies; early testing of lines for general combining ability, using the source population as the tester; intermating remnant S_1 seed of the progenies that had superior performance in the testcross trials; and repeating the procedures for continued selection. Jenkins' (1940) suggestion was based on half-sib family selection that emphasized selection for additive genetic effects. Hull (1945), however, was of the belief that overdominance was of greater importance, and he suggested a recurrent selection scheme that emphasized selection for specific combining ability. The primary difference between the suggestions of Jenkins (1940) and Hull (1945) was the type of testers used to evaluate lines. Because of the conflict between the opposing views on the relative importance of general and specific combining abilities, Comstock et al. (1949) suggested reciprocal recurrent selection, also based on half-sib families, to capitalize on both effects.

Numerous suggestions have been made for conducting recurrent selection in corn (Table 8–10). The first method used by humans for the improvement of corn was simple mass selection based on visual selection for phenotypic differences among individual ears and plants. Except for traits with greater heritabilities (e.g., ear height), simple mass selection generally was not effective (Sprague, 1955). Because of the confounding effects of environment and pollen control, Gardner (1961) suggested modifications to increase the efficiency of mass selection. Ear-to-row selection was designed to base selection on progenies rather than individual plants (Hopkins, 1899). But experimental technique and pollen control also limited its effectiveness. It was not until Lonnquist (1964) and Compton and Comstock (1976) suggested methods of improved experimental techniques and pollen control that ear-to-row selection became an acceptable method for germplasm improvement. Both mass selection and ear-to-row selection have received greater attention in recent years because of improvements to increase the efficiency of selection for determining genetic differences among individuals and progenies.

Most of the other suggested methods of recurrent selection are modifications of the original suggestions of Jenkins (1940), Hull (1945), and Comstock et al. (1949). In most instances, the modifications were made to increase efficiency of selection, based on quantitative genetic theory and data from empirical studies, and to adapt for specific situations. Except for inbred progeny selection, selection is based on either half-sib or full-sib families. Selection based on inbred (S_1 , $S_1 \dots S_n$) progenies has received greater emphasis during the past 10 to 15 yr for the following reasons. Quantitative genetic studies indicated that additive genetic effects with partial to complete dominance were of greater importance than nonadditive effects in corn populations. Hence, selection methods that emphasized selection for additive effects would be appropriate. The coef-

Table 8-10. Recurrent selection methods suggested for the improvement of corn populations.

Method of selection	Progenies evaluated	Progenies used for recombination	Pollen control (c) of progenies recombined	Reference
Intrapopulation				
Mass				
Modified				
Unselected males	Individual plants	Individual plants	Population (c = 0 - 0.5)	Original method Gardner, 1961 Eberhart, 1970
Selected males	Individual plants	Individual plants	Population (c = 0.5)	
	Individual plants	Individual plants	Selected plants (c = 1.0)	
Half-sib				
Ear-to-row	Half-sibs	Half-sibs	Population (c = 0 - 0.5)	Hopkins, 1899
Modified	Half-sibs	Half-sibs	Population (c = 0.5)	Lonnquist, 1964
Modified-modified	Half-sibs	Half-sibs	Selected half-sibs (c = 1.0)	Compton and Comstock, 1976
General combining ability	Half-sibs	Half-sibs		Jenkins, 1940
	Half-sibs	Half-sibs	Selected half-sibs (c = 1.0)	
	Half-sibs	S _i 's	S _i 's of selected half-sibs (c = 2.0)	
Specific combining ability	Half-sibs	Half-sibs	Selected half-sibs (c = 1.0)	Hull, 1945
	Half-sibs	S _i 's	S _i 's of selected half-sibs (c = 2.0)	
Full-sib				
	Full-sibs	Full-sibs	Selected full-sibs (c = 1.0)	Moll and Robinson, 1966 Sprague and Eberhart, 1977
	Full-sibs	S _i 's	S _i 's of selected full-sibs (c = 2.0)	
Inbred				
S ₁	S ₁	S ₁	Selected S ₁ 's (c = 1.0)	Eberhart, 1970
S ₂	S ₂	S ₁ or S ₂	Selected (c = 1.0)	
S _n	S _n	S _n	Selected (c = 1.0)	Brim, 1966
S _n	S _n	S _n	Selected (c = 1.0)	
Single-seed descent				
Interpopulation				
Reciprocal half-sib				
Remnant half-sib	Half-sibs	Half-sibs	Selected half-sibs (c = 1.0)	Comstock et al., 1949
S ₁	Half-sibs	S _i 's	S _i 's of selected half-sibs (c = 2.0)	
Remnant half-sib	Half-sibs	Half-sibs	Selected half-sibs (c = 1.0)	Paterniani and Vencovsky, 1977 Paterniani, 1978
Remnant half-sib	Half-sibs	Half-sibs	Selected half-sibs (c = 0.5)	
Inbred testers	Half-sibs	S _i 's	S _i 's of selected half-sibs (c = 2.0)	Russell and Eberhart, 1975 Comstock, 1979
Reciprocal full-sib				
Full-sib	Full-sibs	S _i 's	S _i 's of selected full-sibs (c = 2.0)	Hallauer and Eberhart, 1970 Marquez-Sanchez, 1982
Full-sib	Full-sibs	Varies	Selected progenies (c = 0.5 - 2.0)	

ficients for the additive genetic component of variance among progenies are 1.0 for S_1 progenies, 1.5 for S_2 progenies, and nearly 2.0 for S_n progenies, but only 0.25 among half-sib and 0.5 among full-sib families. Therefore, the expected genetic variation, assuming only additive genetic effects, among S_1 progenies is expected to be four times greater than among half-sib families and twice that among full-sib families. These expected differences for efficiency of selection also are reflected in the empirical estimates of heritability (Table 8–9). The other reasons for the use of inbred progeny selection are of a practical nature, primarily, for integrating recurrent selection methods with the requirements for applied breeding programs. Inbred recurrent selection usually is restricted to S_1 and S_2 progenies. Inbred progeny selection is effective for exposing deleterious recessive alleles and, consequently, reducing the genetic load of the populations under selection. S_1 progeny selection also is effective for increasing the level of pest resistance. Combinations of S_1 and S_2 progeny selection can be effectively used to screen large (500 to 1000) numbers of S_1 progenies for maturity and pest resistance in one environment and evaluating S_2 progenies, derived from acceptable S_1 progenies, in replicated trials for traits that have lower heritabilities (e.g., yield and lodging resistance). Because single crosses have become of greater importance, greater attention has been given to the vigor and productivity of inbred lines per se to permit their use in the production of hybrid seed. Inbred progeny evaluation, therefore, imposes selection for vigor, standability, and yield. The other important feature of inbred progeny recurrent selection is that it is amenable to applied breeding programs and can be easily integrated with the other aspects of pedigree selection.

The choice of recurrent selection method will be dictated by the objectives for improving populations. Each of the methods, if properly conducted, is effective (Sprague and Eberhart, 1977; Hallauer, 1981; Hallauer and Miranda, 1981; Hallauer, 1985). The choice of selection method probably is not as critical as the choice of population chosen for selection. Mass selection, for example, has been effective in some populations and environments for yield (Johnson, 1963; Gardner, 1977), but it was not effective in other populations and environments (Hallauer and Sears, 1969; Mulamba et al., 1983). Mass selection was effective in modifying plant height (Acosta and Crane, 1972), maturity (Troyer and Brown, 1972; Compton et al., 1979), ear length (Salazar and Hallauer, 1986), and prolificacy (Lonnquist, 1967), but it was not effective for increasing the level of resistance to southwestern corn borer (Williams and Davis, 1983). Similar results can be expected for the other recurrent selection methods. If selection is not effective, the lack of response may be due to either the choice of selection method or the choice of population used. However, a change in selection methods can be made with less disruption in genetic progress than a change in populations. A change in selection methods can be made to increase the efficiency of selection, and the progress made from previous selection is not lost. If, however, one changes populations

included for selection, the genetic gain realized by previous selection will be lost even though the selection method was seemingly ineffective. An unfortunate choice of populations can occur, and it may become evident that the population will not contribute to the breeding program. The only recourse is to discard and start over. Unfortunately, the loss in time and resources can be costly. Choice of germ plasm, therefore, seems more important than choice of recurrent selection method because changes in methods and testers cause little loss in accumulated improvement.

8-2.3 Recurrent Selection—Results

Recurrent selection studies have been conducted in corn since 1939. Data monitoring the response to selection are more extensive for some methods than for others. In several instances, selection was conducted for two or three cycles of selection and discontinued either because the objectives of the program were attained or because of a change in emphasis in the breeding program. For some traits that have a relatively high heritability because of an effective screen, two or three cycles are adequate to achieve the objectives. Some programs were not continued to determine the long-term effects of selection due to the trait under selection, effective population sizes used, effectiveness of different types of testers, and types of genetic effects affected by the selection method. Sprague and Eberhart (1977) and Hallauer and Miranda (1981) presented summaries of the response to selection for different selection methods, primarily for grain yield. Response to selection averaged 2 to 4% per cycle of selection for most recurrent selection methods, emphasizing that recurrent selection, if properly conducted, can effectively increase the frequency of favorable alleles for grain yield. Hence, the choice of method of selection should be dictated by how the method of selection and population under selection contribute to the overall breeding goals.

Some specific examples will be reviewed and summarized to illustrate the types of results obtained by different methods of recurrent selection for different traits. The direct and correlated responses to selection will be included to demonstrate some of the anomalies of selection for specific traits. The differences among the studies are related to the emphasis given to traits under selection, use of effective screens to reduce the confounding effects of genetic and environmental factors, and the correlations between the primary trait of selection and other traits that are important in applied breeding programs.

8-2.3.1 Intrapopulation Selection

Recurrent selection studies conducted within corn populations have been more commonly used because of simplicity, and their applicability for a greater number of traits. They have been particularly effective for improving pest resistance, adapting germ plasm for specific environments, and changing the chemical composition of the grain. Mass, half-

sib family, and S_1 progeny selection are the more commonly used methods with half-sib family selection primarily used for grain yield improvement.

8-2.3.1.1 Mass Selection. The classic mass selection study was conducted in 'Hays Golden'. Gardner (1961) suggested modifications to reduce the effects of environment on selection and to increase parental control with use of adequate isolation. Gardner (1977, 1978) reported a realized gain in grain yield of 3.00% per cycle as a linear response over the first 15 cycles of selection. The realized gain was in excellent agreement with the expected response of 3.08% per cycle. Response to mass selection, however, tended to plateau at cycle 13 and started decreasing at cycle 17. This disturbing trend was discussed relative to possible changes in the original population of Hays Golden, environmental effects experienced because of change in selection sites, changes in genetic variance of the population, and relative importance of nonadditive effects. Although there was some decline in the additive genetic variance with selection, the more plausible explanation was the series of stress environments experienced during the latter cycles of selection (Mareck and Gardner, 1979). Experiments conducted to evaluate selection indicated that the selected cycles did not perform as well in stress environments as the original Hays Golden population. Correlated responses with mass selection for yield included a delay in maturity, an increase in number of ears per plant, and increases in ear and plant height, all of which are often associated with selection that emphasizes increased yield.

Salazar and Hallauer (1986) summarized the direct and correlated responses after 15 cycles of divergent mass selection for ear length, a component of yield. Mass selection for ear length was effective for increased and decreased ear length (Fig. 8-6). Because of the initial composition of the population ('Iowa Long-ear Synthetic'), selection was more

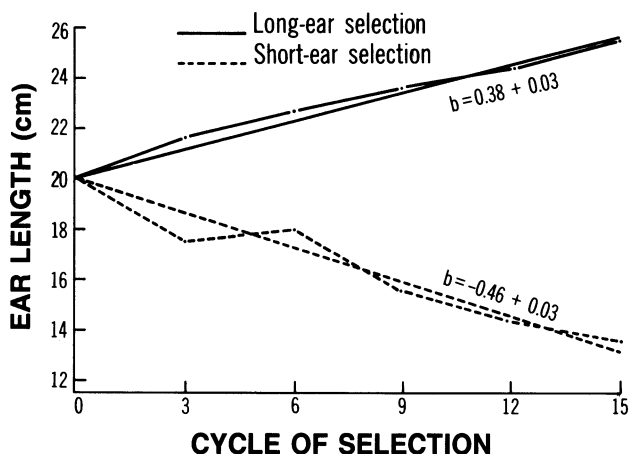


Fig. 8-6. Direct response to divergent mass selection for ear length in Iowa Long Ear Synthetic. Adapted from Salazar and Hallauer (1986).

effective for decreased (-0.46 ± 0.03 cm cycle⁻¹) ear length than for increased (0.38 ± 0.03 cm cycle⁻¹) ear length. Grain yield, as a correlated trait, however, decreased for both selection programs. The decreased yield (-0.044 ± 0.011 Mg ha⁻¹ cycle⁻¹) with selection for increased ear length occurred because kernel depth and number of kernel rows significantly decreased over cycles of selection. Yield decreased because the negative effects of kernel depth and kernel row number negated the effects of increased ear length. Yield decreased (-0.104 ± 0.011 Mg ha⁻¹ cycle⁻¹) at a greater rate with selection for decreased ear length even though there was a significant increase in kernel depth and number of kernel rows. Other correlated effects included later flowering, greater plant height, and greater stalk lodging with mass selection for increased ear length; opposite effects occurred with mass selection for decreased ear length.

Mass selection is effective for a broad range of plant and ear traits (Hallauer and Miranda, 1981). In most instances, single-trait selection was emphasized. Emphasis on selection for only one trait over several (10 to 20) cycles of selection can cause undesirable correlated changes in other traits (e.g., taller, later plants or ears with reduced number of kernel rows and reduced kernel depth). Multiple-trait selection could be used, but this may not be feasible. It seems a good compromise would be to emphasize mass selection initially, and then use some type of family selection to permit greater and effective control for other traits. Mass selection for adaptation, for example, has been effective in populations that include exotic germ plasm (Compton et al., 1979). After the populations have acceptable standards for use within certain areas, other breeding and selection methods can be used to control maturity, plant stature, and ear size.

Selection for percentage of oil and protein of the seed was initiated in 1896 in the open-pollinated cv. Burr's White. This is the longest continuous selection program conducted in corn, and details of the study after 76 generations of selection were reported by Dudley (1977). Divergent selection for oil and protein content was initiated by analyzing 163 open-pollinated ears (half-sib families). The 24 ears highest in protein and oil and the 12 lowest in protein and oil were used to initiate selection for strains with higher protein (IHP) and oil (IHO) and strains with lower protein (ILP) and oil (ILO). During the course of selection, different strains were developed to determine if adequate genetic variation was present for reverse selection within the respective high and low strains for protein and oil. Selection was effective in all instances. Gains after the completion of 76 generations were 292 (IHO), 92 (ILO), 133 (IHP), and 78% (ILP). Dudley and Lambert (1969) determined that significant estimates of genetic variation among half-sib families for the selected traits existed after 65 generations of selection in each of the strains. Dudley (1977) concluded that the realized gains were explainable when reasonable allele frequencies and numbers of loci involved were assumed. Frequencies of favorable alleles in the original Burr White were estimated

at <0.37 for percentage of protein and <0.25 for percentage of oil. A minimum of 54 loci were estimated to differentiate IHO and ILO and a minimum of 122 loci to differentiate IHP and ILP.

Dudley (1977) discussed the results of selection for kernel oil and protein concentration relative to the genetic variation available for genetic improvement of corn. It does not seem the lack of genetic variation in corn should be a constraint for continued genetic improvement. One would assume there are more loci segregating for yield in corn populations than there were in Burr's White for percentage of oil and protein. If the yield of a corn population could be increased three to four times its original mean, as was the case for IHO and IHP, selected populations could be expected to have yields in excess of 18.8 Mg ha^{-1} . If allele frequencies were between 0.25 and 0.5 for 50 to 200 loci to permit a gain of $20 \sigma_A$, there seems to be little concern about exhausting genetic variability for grain yield in corn. Dudley (1977) concluded that the greater concern seems to be developing methods to increase the efficiency of concentrating favorable alleles rather than whether sufficient genetic variability is available.

8-2.3.1.2 S_1 Progeny Recurrent Selection. Devey and Russell (1983) summarized the effects of seven cycles of selection for improved stalk quality in the open-pollinated cv. Lancaster, which was designated as BSL(S). BSL(S)C1 through BSL(S)C4 were selected on the basis of S_0 plant and S_1 progeny resistance to stalk-rot development following artificial inoculation with *Diplodia maydis* (Berk.) Sacc. After four cycles of selection, Jinahyon and Russell (1969) concluded that further gains for stalk quality based on stalk-rot resistance would be small. At this time, selection that emphasized greater mechanical strength of the stalk was initiated. BSL(S)C5 through BSL(S)C7 were derived on the basis of S_0 plant selection for stalk-rot resistance and S_1 progeny performance for improved mechanical stalk strength. After the completion of seven cycles of selection for stalk quality, the original Lancaster population (C0) and seven successively improved populations (C1 through C7) were evaluated for stalk-rot infection and mechanical stalk strength.

The incidence of stalk-rot infection and level of mechanical stalk strength in cycles of selection for improved stalk quality in the Lancaster population are illustrated in Fig. 8-7. The incidence of stalk-rot infections significantly decreased ($b = -0.26 \pm 0.03$) over the seven cycles of selection with similar rates of gain for stalk-rot resistance based on selection for stalk-rot resistance in the first four cycles ($b = -0.27$) and mechanical stalk strength the last three cycles ($b = -0.28$). On a scale of 0.5 (no spread of disease) to 6 (premature death of plant), the level of stalk-rot infection decreased from 3.27 for the C0 to 1.33 for the C7, which compared favorably with 1.44 for the resistant check, B14A $\times$ C103. The progress for continued decrease in stalk-rot infection with selection for greater mechanical stalk strength suggests a close association between stalk-rot resistance and morphological stalk traits that contrib-

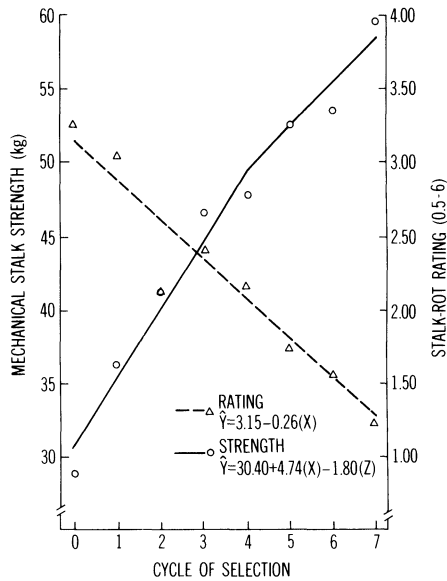


Fig. 8-7. Regression of stalk-rot rating and mechanical stalk strength on cycles of selection for Lancaster. Adapted from Devey and Russell (1983).

uted to mechanical stalk strength. Mechanical stalk strength increased from 28.7 kg for the C0 to 47.9 kg for the C4 and 59.6 kg in the C7. The estimated gain in mechanical stalk strength was 4.75 kg from C0 to C4 and 2.95 kg from C4 to C7 with 97.5% of variation among populations explained by fitting the two linear regressions.

In addition to determining the direct effects of selection for improved stalk quality, Devey and Russell (1983) also measured other plant and ear traits for the C0 through C7 (Table 8-11). Comparisons of the C7 relative to the C0 showed that selection for increased stalk strength significantly delayed flowering (5-6 d), increased plant height (11.3 cm) and internode number (1.6), and decreased internode length (1.1 cm). Average stalk lodging decreased from 31.6% in the C0 to 0.3% in the C7, compared with 1.2% for the resistant check, B14A $\times$ C103. Except for the delay in flowering and increased plant height, the correlated changes for the other traits with selection for improved stalk quality should not be critical. The greatest detrimental effects, however, were the correlated changes in grain yield and the components of yield. Yield decreased 40% from the C0 (6.65 Mg ha⁻¹) to the C7 (4.01 Mg ha⁻¹). Grain yield was maintained for the first three cycles of selection, but decreased rapidly after the C3. The 40% decrease in grain yield was reflected in each of the components with ears per plant accounting for most of the decrease in yield.

Because of the methods used for discriminating among plants and S₁ progenies, selection was effective for improving stalk quality but the correlated changes were not desirable, particularly for later maturity and reduced grain yield. Greater yields usually are correlated with later maturity. Hence, the other associated changes were too great to take ad-

Table 8-11. Means and regression coefficients for eight traits after seven cycles of recurrent selection for stalk quality in Lancaster. Adapted from Devey and Russell (1983).

Cycle of selection	Yield	Days to pollen shed†	Plant ht.	Internode		Ears per 100 plants	Kernel-row no.	Ear length
				No.	Length			
	Mg ha ⁻¹	no.	cm	no.	cm	— no. —		cm
0	6.65	16.0	244	13.7	17.9	94.5	14.5	19.0
1	6.63	18.6	262	14.4	18.3	93.0	14.8	19.0
2	6.63	19.3	267	15.2	17.7	97.5	13.9	18.6
3	6.18	18.9	264	15.1	17.6	93.0	12.8	19.3
4	5.44	18.4	252	14.6	17.3	91.5	13.4	18.0
5	5.02	18.7	248	14.8	16.8	88.5	12.4	17.4
6	4.69	20.4	256	15.3	16.9	81.0	13.2	15.6
7	4.01	21.8	255	15.3	16.8	75.5	13.1	13.9
b/‡	-0.115**	2.7**	22*	1.2**	2.4**	NS	-0.74**	-0.13**

*,** Significantly different from zero at the 0.05 and 0.01 levels, respectively.

† Beginning at 1 July.

‡ Estimates were obtained by multiple regression analysis with C4 being the joining point for the polynomials. C4 is where the selection was changed from ratings for stalk-rot infection to ratings for mechanical strength of stalks.

vantage of the later maturity. Devey and Russell (1983) suggested that the confounding effects of inbreeding depression due to small effective population size and changes in the partitioning of photosynthate, originally suggested by Dodd (1980), were the major causes for the decline in yield.

The S₁ recurrent selection program for improved stalk quality illustrates the advantages and disadvantages of the method. Selection was effective because methods for discrimination among plants and progenies for the trait of interest minimized escapes; i.e., effective screens were available. Single-trait selection, however, has obvious disadvantages for developing populations for applied breeding programs. Because effective screens are available for stalk quality, attention also needs to be given to other important traits, such as maturity and grain yield. Larger number of progenies could be included with less emphasis given to stalk quality. The rate of increase for stalk quality would be slower, but acceptable levels of maturity and grain yield could be maintained. Use of a selection index for the primary traits of interest and greater effective population sizes would be needed to reduce the undesirable effects of single-trait selection.

Penny et al. (1967) reported results from S₁ recurrent selection for leaf-feeding resistance to the European corn borer conducted in five synthetic varieties. Three cycles of selection were completed. Manual infestation of artificially reared corn borer eggs was used in each cycle of selection for each population. After the completion of three cycles of selection, 100 S₁ progenies were extracted from the C0, C1, C2, and C3 of each population and evaluated in three-replicate trials with manual infestation of corn borer egg masses. Three cycles of S₁ recurrent selection

were found to be adequate to provide S_1 progenies with an acceptable level of resistance to the first-generation European corn borer. On the average, S_1 progeny ratings were reduced from 5.4 to 2.5 (1 = resistant and 9 = susceptible) with 77% of the S_1 progenies included within the resistant classes. Penny et al. (1967) concluded that differences among S_1 progenies were present after three cycles of selection, but that the nine-class visual rating scale probably was not adequate to detect individual progenies that included the greatest number of resistance genes. Russell et al. (1979) observed significant correlated changes in other agronomic traits.

The European corn borer normally has two generations per year in Iowa. Acceptable levels of resistance to first-generation feeding have been identified in most germplasm sources tested, but identifying resistance to second-generation feeding has been more difficult because methods of infestation are more difficult and time consuming and most germplasm sources have a lower frequency of factors that contribute to resistance. Klenke et al. (1986) conducted a recurrent selection study to select for resistance to both generations of feeding in BS9, a synthetic developed by intermating 10 inbred lines selected on the basis of their combining abilities and resistance to both generations of the European corn borer. General objective of the study was to determine if selection methods were effective in developing resistance to the European corn borer for the whole life of the corn plant.

S_1 recurrent selection was used with artificial infestation for both generations. After the completion of four cycles of selection, the five populations of BS9 (C0, C1, C2, C3, and C4) and the five populations crossed to four testers were evaluated to determine progress achieved in BS9 by S_1 recurrent selection and to assess worth of resistance in reducing yield losses due to infestation.

Selection was effective in reducing the level of infestation for both generations (Table 8-12). The level of infestation in the C4 was significantly less than in the BS9C0 in all instances: first-generation feeding was reduced 25% after four cycles of selection and second-generation feeding was reduced 31%. Visual ratings for second-generation feeding were corroborated by nearly a 60% reduction in cavity counts from C0 to the C4. The methods used to increase the levels of resistance were effective in BS9 even though BS9 was synthesized by intermating lines that possessed resistance to infestation by either one or both generations of European corn borer (Klenke et al., 1986). Increased levels of resistance, however, were obtained at the expense of grain yield (Table 8-12). Yield of the noninfested control populations was reduced 31.1%, comparing the yield of the C4 relative to the C0. Yields of the C4 populations infested for first- and second-generation corn borers also were reduced 21.2 to 31.8%. Genetic factors that contributed to European corn borer resistance throughout the life of the corn plant also must have affected physiological processes that are important for either the synthesis and translocation of

Table 8-12. European corn borer ratings and grain yield for BS9 and for four-cycle populations after S₁ recurrent selection for first- and second-generation resistance. Adapted from Klenke et al (1986).

Populations	Control‡	Treatments†							
		FGI		SGI		FGI & SGI		CVC	
		Rating	Yield	Rating	Yield	Rating§	Yield	SCI	FGI & SGI
	Mg ha ⁻¹	1-9¶	Mg ha ⁻¹	1-9¶	Mg ha ⁻¹	1-9¶	Mg ha ⁻¹	no.	
BS9CO	6.97	3.6	6.07	6.4	5.31	6.3	4.90	8.9	8.0
C1	6.34	3.6	6.50	5.9	4.75	6.2	4.87	8.7	7.1
C2	6.03	2.8	5.24	5.7	4.44	5.2	4.87	5.7	5.0
C3	5.53	2.5	5.62	4.4	4.08	4.4	4.78	3.9	4.8
C4	4.80	2.7	4.79	4.4	4.40	4.3	4.41	3.1	3.4
LSD (0.05)	1.38	0.8	1.38	1.3	1.38	1.3	1.38	2.2	2.2
Change, #	-31.1	-25.0	-21.1	-31.2	-17.1	-31.8	-10.0	-65.2	-57.5

† Abbreviations for treatments: FGI = first generation infestation; SGI = second generation infestation; and CVC = cavity counts with one cavity = 2.5 cm.

‡ Populations were not infested and were sprayed with carbofuran to control natural infestation.

§ Second generation rating.

¶ Visual ratings on 1 (resistant) to 9 (susceptible) scale.

Change of C4 relative to CO.

photosynthates or the number or size of kernels. Corn borer resistance contributes to improved plant health and has been one factor that has contributed to the genetic gains experienced in the newer hybrids (Duvick, 1984). The results of Klenke et al. (1986) are similar to those reported by Devey and Russell (1983) for improved stalk quality. High selection pressures for a single trait were effective, but the correlated responses for other important traits were not desirable.

Because of the expansion of corn growing areas in higher latitudes and elevations and the changes in tillage practices used in corn production, increased attention has been given to corn genotypes that germinate and grow in cooler soil environments. S_1 progeny recurrent selection has been used to select for greater cold tolerance in possible germplasm sources. Mock and Bakri (1976) evaluated BS13(SCT) after two cycles and BSSS2(SCT) after three cycles of S_1 progeny selection for cold tolerance. S_1 progeny selection improved percentage of emergence 30.1% and seedling dry weight 13.2% in BS13(SCT) with no improvement in BSSS2(SCT). Hoard and Crosbie (1985) evaluated BS13(SCT) and BSSS2(SCT) after five cycles of selection and reported average changes for the two populations as 2.1% cycle⁻¹ for percentage of emergence, 0.04 g cycle⁻¹ for seedling dry weight, and 0.3 units cycle⁻¹ for seedling vigor score. Hoard and Crosbie (1985) concluded that selection would be effective with use of a selection index that included percentage of emergence and seedling dry weight, using data from more than one environment.

8-2.3.1.3 Half-sib Family and Inbred Progeny Selection. BSK is a strain of the open-pollinated cv. Krug Yellow Dent that was developed at the Nebraska Agricultural Experiment Station and designated 'Krug High I Syn. 3' (Lonnquist, 1949). In 1953, S_1 progeny and half-sib family recurrent selection for grain yield were initiated in BSK; the two strains of BSK were designated BSK(S) for S_1 progeny selection and BSK(HI) for half-sib family selection. S_1 progenies per se were tested for the first six cycles, and S_2 progenies per se for cycles 7 and 8 for BSK(S). In BSK(HI), different testers were used for different cycles of selection. The double-cross Ia4652 [(WF9 × W22) × (B14 × M14)] was used as the tester for the first three cycles, and the two parental single crosses of Ia4652 served as the testers for cycles 4 and 5. For the sixth cycle, a low-yielding related line, 'Krug 755', was used as the tester. An unrelated elite line, B73, was used as tester for cycles 7 and 8. Yield was the primary trait of selection, but attention also was given to lodging and grain moisture at harvest.

Smith (1979b) and Tanner and Smith (1987) conducted studies to determine response to selection for both methods of recurrent selection (Table 8-13). The evaluation study included populations per se, populations per se selfed one generation, population crosses between the cycle populations for both methods of selection, and population crosses selfed one generation. Positive response to selection for grain yield was realized in all comparisons (Table 8-13). After eight cycles of selection, BSK(S)C8

had 23.4% greater yield, and BSK(HI)C8 had 32.4% greater yield than BSKC0. Yield increases over cycles of selection between the two methods of selection, however, were different. The greatest yield in BSK(S) was obtained by the C4 with no further gains with four additional cycles of selection. With half-sib family selection, significant gains in grain yield were realized from the C4 to the C8. Because of the restricted genetic base of the BSKC0 population and the small effective population sizes ($N_e = 10$) used in recombination, the different rates of response among cycles of S_1 - S_2 progeny and half-sib family selection may be expected. Tanner and Smith (1987) estimated the effects due to finite population

Table 8-13. Response for six traits from half-sib (HI) and S_1 (S) recurrent selection conducted in Krug Hi I Syn. 3 (BSK), their crosses, and after one generation of selfing in the populations and crosses. Adapted from Tanner and Smith (1987).

Cycle of selection	BSK(S)		BSK(S) $\times$ BSK(HI)		BSK(HI)	
	Per se	Self	Per se	Self	Per se	Self
Yield, LSD (0.05) = 0.79 Mg ha ⁻¹						
C0	4.87	2.77	4.87	2.77	4.87	2.77
C4	6.21	3.90	6.16	4.08	5.29	3.19
C8	6.01	4.13	7.11	4.36	6.45	3.91
†	23.4	49.1	46.0	57.4	32.4	41.2
Grain moisture, LSD (0.05) = 1.3%						
C0	22.1	22.4	22.1	22.4	22.1	22.4
C4	21.7	22.1	21.8	21.8	21.8	22.4
C8	22.1	21.7	22.2	22.2	23.4	22.8
†	0.0	-3.2	0.4	-0.9	0.06	1.8
Root lodging, LSD (0.05) = 10.0%						
C0	25.6	24.4	25.6	24.4	25.6	24.4
C4	8.9	5.8	15.0	17.1	25.3	24.0
C8	2.6	2.4	9.5	5.2	17.0	15.1
†	-89.8	-90.2	-62.9	-78.7	-33.6	-38.1
Stalk lodging, LSD (0.05) = 8.9%						
C0	41.4	40.4	41.4	40.4	41.4	40.4
C4	39.0	41.0	48.7	46.8	39.9	39.8
C8	51.7	49.9	46.0	49.1	36.0	34.1
†	24.9	23.5	11.1	21.5	-13.0	-15.6
Plant height, LSD (0.05) = 9.4 cm						
C0	232	210	232	210	232	210
C4	227	209	231	212	230	216
C8	227	210	234	195	213	200
†	-1.2	0.0	0.9	-7.2	-8.2	-4.8
Days to pollen shed, LSD (0.05) = 1.9 d‡						
C0	21.5	23.8	21.5	23.8	21.5	23.8
C4	19.8	21.0	19.0	22.5	20.5	22.8
C8	20.3	21.8	17.5	20.5	20.6	22.5
†	-5.6	-8.4	-18.6	-13.9	-4.2	-5.5

† Percentage change for C8 relative to C0.

‡ Beginning at 1 July.

size for BSK(S) and BSK(HI). The cumulative effects of inbreeding due to finite population size over eight cycles of selection were expected to decrease observed gain in the populations per se by 2.24 Mg ha^{-1} in BSK(S) and 1.15 Mg ha^{-1} in BSK(HI). The larger effects of finite population size in BSK(S) were attributed to recombination of S_2 progenies in C7 and C8 and the greater effectiveness of S_1 and S_2 selection in eliminating deleterious recessive alleles in BSK(S). The larger effects of drift in BSK(S) and the increased efficiency of BSK(HI) in later cycles resulted in a crossover of observed yield response (Table 8–13).

The greater effectiveness of S_1 and S_2 progeny selection in eliminating deleterious alleles also is reflected in the S_1 generation performance of the populations per se. Both methods of selection reduced inbreeding depression in the C8 compared with the C0; however, inbreeding depression was 7.9% less after eight cycles of S_1 and S_2 progeny selection compared with half-sib family selection (Table 8–13). Inbreeding depression after four cycles of S_1 progeny selection (3.90 Mg ha^{-1}) was similar to eight cycles of half-sib family selection (3.91 Mg ha^{-1}).

Crosses of populations after four and eight cycles of selection suggest that the two methods of selection increased the frequencies of different alleles. Mid-parent heterosis was 7.1% after four cycles of selection and 14.1% after eight cycles. The $C4 \times C4$ cross yield (6.16 Mg ha^{-1}) was similar to BSK(S)C4 (6.21 Mg ha^{-1}). After eight cycles of selection, the $C8 \times C8$ cross yielded 7.11 Mg ha^{-1} as compared with 6.01 Mg ha^{-1} for BSK(S)C8 and 6.45 Mg ha^{-1} for BSK(HI)C8. Inbreeding depression of the S_1 generation of the population crosses was similar to that for BSK(S). Inbreeding depression for the S_1 generation of BSK(S)C8 $\times$ BSK(HI)C8 was reduced 57.4% compared with the S_1 generation of BSKC0. S_1 and S_2 progeny selection were more effective, as expected, than half-sib selection for reducing the effects of inbreeding.

Except for root and stalk lodging, effective selection for greater grain yield by inbred progeny and half-sib family selection did not result in undesirable correlated responses for the other traits of interest to breeders. Changes observed with selection for grain yield did not result in taller plants with delayed maturity. Root and stalk quality are important traits in applied breeding programs, and BSK(S)C8 and BSK(HI)C8 do not have acceptable levels of root and stalk quality. Except for stalk quality in BSK(S), the observed trends are in the desired direction (Table 8–13). S_1 and S_2 progeny selection were more effective than half-sib family selection for improved root quality, but S_1 and S_2 progeny selection was not as effective as half-sib family selection for stalk lodging resistance. Stalk lodging significantly increased 24.9% in BSK(S)C8, whereas there was a nonsignificant decrease of 13.0% in BSK(HI)C8. It is not clear why the reverse trends were observed for root and stalk lodging for inbred progeny vs. half-sib family selection. Similar experimental procedures and test environments were used for both selection programs, but selection among S_1 progenies was not effective. Selection for greater yield

among S_1 and S_2 progenies seemingly directed a greater portion of photosynthate to the grain, which is the opposite effect experienced by Devey and Russell (1983) who emphasized selection for greater stalk quality (Table 8-11).

The response to eight cycles of selection for greater grain yield by inbred progeny (2.9% cycle⁻¹) and half-sib family (4.0% cycle⁻¹) recurrent selection in BSK was similar although the rates of response varied among cycles. Except for root and stalk lodging, the indirect effects of selection also were similar for both methods. The responses to selection for the primary trait were similar to the summaries reported by Sprague and Eberhart (1977) and Hallauer and Miranda (1981). Hence, the choice of method of selection was not critical.

Mulamba et al. (1983) tested S_1 progenies extracted from BSKC0, BSK(S)C8, BSK(HI)C8, and BSK(M)C14. BSK(M)C14 was derived from BSKC0 by 14 cycles of mass selection for grain yield. BSK(M)C14 had 8.25% greater yield than BSKC0, or 0.58% gain per cycle of mass selection. One-hundred S_1 progenies were obtained from BSKC0, BSK(S)C8, BSK(HI)C8, and BSK(M)C14 and evaluated in four environments (Table 8-14). The relative changes for the means of the 100 S_1 progenies for BSK(S)C8 and BSK(HI)C8 were similar to the selfed generations shown in Table 8-13 for most traits. Eight cycles of inbred progeny and half-sib family selection were more efficient than 14 cycles of mass selection for developing germplasm sources for breeding programs. S_1 progenies extracted from BSK(M)C14 were lower yielding, later in maturity, and taller than the S_1 progenies extracted from BSK(S)C8 and BSK(HI)C8. The main disturbing feature of the progeny selection methods is the tendency to have lower estimates of σ_G^2 after eight cycles of selection, particularly for BSK(S)C8. The estimate of σ_G^2 among S_1 progenies of BSK(S)C8 agrees with the findings of Tanner and Smith (1987) that the cumulative effects of inbreeding were greater in BSK(S) than in BSK(HI).

Studies comparing the relative effectiveness of half-sib family and inbred progeny selection have been reported by Horner et al. (1973), Horner et al. (1976), Horner (1985), and Zambezi et al. (1986). Objectives of the studies were to compare the relative effectiveness of half-sib family selection with different types of testers (inbred lines, single crosses, and genetically broad base composite) and S_2 progeny selection in the improvement of populations themselves, populations selfed, and testcrosses to different types of testers. Grain yield was the primary trait of selection, but some attention also was given to lodging, ear height, and ear number. Because selfed-progeny selection is expected to be more effective than half-sib family selection, they were also interested in evaluating the relative efficiency of the two methods for changing allelic frequencies in the populations.

Horner et al. (1973) reported data for three concurrent recurrent selection methods (half-sib family with inbred and broad-based population as testers and S_2 progeny per se) following the suggestion of Hull (1952).

Table 8-14. Mean ($\bar{x}$), standard deviation of means (SD), ranges, and estimates of variability (σ^2_G) for six traits measured on 100 S_1 progenies of four BSK populations. Adapted from Mulamba et al. (1983).

Traits	Populations†	$\bar{x} \pm \text{SD}$	Percentage of C0	Range	σ^2_G
Yield, Mg ha ⁻¹	BSKC0	2.91 $\pm$ 0.06	--	0.49-5.72	62.5 $\pm$ 11.1
	BSK(M)C14	2.71 $\pm$ 0.06	93.1	0.88-4.37	65.5 $\pm$ 11.5
	BSK(HI)C8	4.74 $\pm$ 0.05	163.0	3.20-7.99	52.9 $\pm$ 8.5
	BSK(S)C8	4.94 $\pm$ 0.05	170.0	3.23-6.69	28.0 $\pm$ 6.1
Grain moisture, %	BSKC0	16.8 $\pm$ 0.11	--	14.3-19.8	0.7 $\pm$ 0.2
	BSK(M)C14	18.2 $\pm$ 0.16	108.0	15.4-22.2	1.7 $\pm$ 0.3
	BSK(HI)C8	18.5 $\pm$ 0.13	109.8	15.8-21.1	1.1 $\pm$ 0.3
	BSK(S)C8	17.5 $\pm$ 0.11	104.1	15.1-21.4	0.6 $\pm$ 0.2
Root lodging, %	BSKC0	13.2 $\pm$ 0.33	--	7.2-20.0	6.6 $\pm$ 1.4
	BSK(M)C14	12.9 $\pm$ 0.31	97.4	7.2-21.6	4.8 $\pm$ 1.2
	BSK(HI)C8	11.0 $\pm$ 0.36	83.2	6.3-22.9	9.3 $\pm$ 1.7
	BSK(S)C8	8.3 $\pm$ 0.18	62.8	5.9-13.9	2.2 $\pm$ 0.4
Stalk lodging, %	BSKC0	10.5 $\pm$ 0.21	--	6.4-16.8	2.6 $\pm$ 0.6
	BSK(M)C14	11.9 $\pm$ 0.28	113.3	6.2-23.1	4.7 $\pm$ 1.1
	BSK(HI)C8	9.5 $\pm$ 0.16	90.0	6.0-13.6	1.1 $\pm$ 0.4
	BSK(S)C8	10.3 $\pm$ 0.20	97.8	6.8-16.2	1.8 $\pm$ 0.6
Ear height, cm	BSKC0	112.2 $\pm$ 1.17	--	80.5-137.8	128 $\pm$ 21
	BSK(M)C14	134.0 $\pm$ 1.56	119.4	96.0-166.2	206 $\pm$ 33
	BSK(HI)C8	94.8 $\pm$ 1.12	84.5	67.8-125.8	44 $\pm$ 16
	BSK(S)C8	95.6 $\pm$ 1.03	85.2	69.0-123.0	93 $\pm$ 15
Days to silk, no.	BSKC0	90.3 $\pm$ 0.45	--	83.0-105.3	16.6 $\pm$ 3.0
	BSK(M)C14	96.7 $\pm$ 0.34	107.1	87.7-104.0	9.5 $\pm$ 1.8
	BSK(HI)C8	85.1 $\pm$ 0.28	94.4	79.3-95.5	6.4 $\pm$ 1.1
	BSK(S)C8	83.7 $\pm$ 0.25	92.7	79.5-91.7	4.9 $\pm$ 0.9

† BSKC0 is the original unselected population; BSK(M)C14 after 14 cycles of mass selection for yield; BSK(HI)C8 after eight cycles of half-sib family selection for yield; and BSK(S)C8 after eight cycles of S_1 progeny selection for yield.

Fla. 767 was the original source population. F6 was the inbred tester and Fla. 767 the broad-based tester. After five cycles of selection for each method were completed, selected populations for each method were crossed to two testers Fla. 767, the original population, and Fla. 3W, an unrelated synthetic, both of which are genetically broad-based populations. Significant linear increases in general combining ability were obtained with each method of selection, but the inbred tester method (4.4% cycle⁻¹) was more effective than the use of parental population as tester (2.4% cycle⁻¹) and S_2 progeny (2.0% cycle⁻¹) selection. Because the rate of response with use of an inbred as tester was twice the rate from S_2 progeny selection, they suggested that the inbred tester was homozygous recessive at many important loci, and, consequently, the inbred tester would have greater variation among testcrosses than the original population, which probably has intermediate allelic frequencies at most loci. The average testcross variances after five cycles of selection were 5.3 for F6 and 2.0 for Fla. 767; thus variation among F6 testcrosses was 2.65 times greater than among Fla. 767 testcrosses. Variability among S_2 prog-

enies averaged over five cycles was 19.4, nearly four times greater than among F6 testcrosses. Hence, it seems progress for population per se should have been more effective with S_2 progeny selection than with testcross selection. It seemed, however, that S_2 progeny selection was not as effective in fixing dominant favorable alleles that combined well with the testers.

Horner et al. (1976) reported on the effectiveness of a single-cross ($F44 \times F6$) tester for the improvement of combining ability. The source population also was Fla. 767 and six cycles of half-sib family selection were evaluated in testcrosses with $F44 \times F6$, the tester used in selection, and FS3W, an unrelated synthetic variety. Performance over cycles of selection were similar for both testers with 18% greater grain yield, 9% lower ear height, and 35% less lodging. Horner et al. (1976) concluded that half-sib family selection increased the frequency of genes with additive effects; testers that have a genetically narrow base (i.e., single-cross hybrid) are effective for improving general as well as specific combining ability; and that it is possible to change testers in recurrent selection programs with little loss in accumulated gain.

Because the improvement in general combining ability during five cycles of selection in Fla. 767 from use of inbred F6 as tester was nearly two times greater than from the use of the parent population (Fla. 767) as tester and S_2 progeny selection, Horner (1985) reexamined the comparisons of testcross vs. S_2 progeny selection in subpopulations (A and B) derived from a different genetically broad-base synthetic, FSHmR. Grain yield was the primary trait of selection, and three cycles were completed for each method of selection. Evaluation trials to estimate response to selection indicated significant progress for both methods with no overall significant differences between testcross and S_2 selection (Table 8–15). The highest average gain ($6.6\% \text{ cycle}^{-1}$) was for the population crosses, which included the selected cycles for the two subpopulations A and B. For the average comparisons of combining ability for grain yield for three testers, gains per cycle of $4.0\% (0.19 \text{ Mg ha}^{-1})$ for S_2 progeny selection and $4.6\% (0.21 \text{ Mg ha}^{-1})$ for testcross selection were not significantly different. The testers included the populations and two inbred testers, one used for testcross selection and one unrelated. There was no consistent trend for combining ability between the types of testers. Zambezi et al.'s (1986) study also included genetically narrow- and broad-based testers and their data also provided further evidence that inbred testers can be used for improving general as well as specific combining ability in corn. Performance of the third-cycle populations at three levels of inbreeding (Syn-1, S_1 , and S_2) indicate that S_2 progeny selection resulted in less inbreeding depression than the testcross method. Estimated rates of inbreeding depression were $-0.049 \text{ Mg ha}^{-1}$ for S_2 progeny selection and $-0.057 \text{ Mg ha}^{-1}$ for testcross selection (Table 8–15). Inbreeding depression was significantly less with S_2 selection, and the predicted yields of homozygous lines were 2.22 Mg ha^{-1} for S_2 progeny selection and 1.47

Table 8-15. Effects of testcross (TC) and S_2 recurrent selection on grain yield. Adapted from Horner (1985).

Populations and method	$C_n \times C_n$ crosses [†]	Testcross means [‡]	Bulks of selfing in C3			
			Syn. 1	S_1	S_2	S_6
			Mg ha ⁻¹			
C0	4.71	4.91	--	--	--	--
C1, S2	4.94	5.00	--	--	--	--
C3, S2	5.61	5.50	6.88	4.56	3.16	2.22§
b_1	0.28**	0.19**	--	--	--	-0.049¶
C1, TC	5.28	5.15	--	--	--	--
C3, TC	5.68	5.55	6.72	4.28	2.69	1.47§
b	0.34**	0.22**	--	--	--	-0.057¶
LSD (0.05)	0.31	0.21	0.62	0.31	0.31	--

** Significantly different from zero at the 1% level.

† Crosses between A and B subpopulations.

‡ Average for A and B subpopulations crossed to C0 and two inbred testers.

§ Predicted yields of homozygous lines.

¶ Rate of inbreeding depression.

Mg ha⁻¹ for testcross selection. Hence, the differences between methods for combining ability were not significant, but less inbreeding depression was expressed in populations improved by S_2 progeny selection.

Other selection programs have compared relative gains realized from S_2 progeny and half-sib family selection. In some instances, only one to three cycles of selection were completed, and the types of testers used have ranged from elite inbred lines to unimproved, open-pollinated varieties. Results and conclusions from the studies were not conclusive in that neither method was clearly superior to the other (Hallauer and Miranda, 1981). In the absence of overdominance, inbred progeny selection is expected to be superior to half-sib (or testcross) family selection for changing allelic frequencies in a population (Comstock, 1964; Wright, 1980). Theoretically, genetic variation among S_1 progenies is expected to be four times greater than among half-sib families when gene frequency is 0.5 and six times greater if S_2 progeny selection were used. Most of the evidence in corn populations suggests that genetic variation for yield in corn is primarily additive, but this does not eliminate the possibility of nonadditive variation at some loci, particularly in elite germ plasm. Under these conditions, inbred progeny selection should be more effective than half-sib family selection, which has not always been the case. The following conclusions seem valid and reasonable for the data reported for comparisons of inbred progeny and half-sib family recurrent selection: populations have responded to selection by both methods with no consistent advantage for either method; inbreeding depression was less in populations improved by inbred progeny selection and this is expected because inbred selection emphasizes contributions to homozygous loci; there was no clear evidence that combining ability was different for the two methods, though inbred progeny selection does not include testcross

information in making selection; rate of response may differ among the cycles of selection for the two methods (e.g., Tanner, 1984); the choice of testers does not seem to influence response to half-sib family selection (i.e., inbred line or genetically broad-base populations); and it is possible to change testers during the sequence of selection cycles with little loss in accumulated gains. If, however, overdominance becomes of greater importance in later cycles, half-sib family selection may prove to be more effective. Jensen et al. (1983) reported S_2 progeny selection was not effective in their elite germ plasm because of nonadditive effects.

8-2.3.1.4 Iowa Stiff Stalk Synthetic. Half-sib family and inbred progeny (S_1 and S_2) selection have been conducted in Iowa Stiff Stalk Synthetic (BSSS), but both methods were not conducted concurrently as for BSK and Fla. 767. The first sampling for half-sib family selection was in 1939 with the double-cross, Ia13 [(L317 $\times$ BL349) $\times$ (BL345 $\times$ MC401)] as the tester. After the completion of seven cycles of half-sib family selection, S_1 and S_2 progeny selection were initiated in BS13(HT)C7 to increase the variability among progenies evaluated. Details of the half-sib family selection program were provided by Eberhart et al. (1973), and estimates of the response to selection were presented by Eberhart et al. (1973), Smith (1979a, 1983, 1984), and Hallauer et al. (1983). Briefly, the response to selection in testcrosses with the tester, Ia13, (18.5%) was about 7% greater than the testcrosses of the improved cycles with BSSSC0 as tester (11.9%) and nearly 10% greater than populations per se (8.9%) for grain yield. Response to selection for improved grain yield per cycle was 0.072 Mg ha⁻¹ for populations per se, 0.092 Mg ha⁻¹ for BSSSC0 testcrosses, and 0.165 Mg ha⁻¹ for Ia13 testcrosses. Response to selection was significant in all instances for half-sib family selection in BSSS, but Smith (1983) also estimated a significant inbreeding effect (-0.113 ± 0.047 Mg ha⁻¹) in BS13(HT) because only 10 S_1 lines were used in recombination.

Inbred progeny (S_1 and S_2) selection was initiated in BS13(HT)C7, and the population was redesignated as BS13(S)C0. Four cycles of inbred progeny selection have been completed, and Helms (1986) evaluated response to selection after seven cycles of half-sib family and four cycles of inbred progeny selection (Tables 8-16 and 8-17). Helms (1986) also included populations derived from BSSSC0 by reciprocal recurrent selection with BSCB1. Grain yield increased 38.2% after 11 cycles of selection, but 36.9% of the gain was achieved with seven cycles of half-sib family selection (BS13C0) and only 1.3% with inbred progeny selection [BS13C0 vs. BS13(S)C4]. The 11 cycles of intrapopulation selection that emphasized grain yield in BSSSC0 were similar to the 10 cycles of interpopulation half-sib selection (38.2% vs. 37.9%, Table 8-16). In both selection programs, most of the gain was realized after six cycles of selection. The main effects of the four cycles of inbred progeny selection in BS13(S) seemed to be greater fixation of favorable alleles in the homozygous state: inbreeding depression of BSSSC0 (34.8%) and BS13(S)C0

Table 8-16. Observed responses for four traits of populations per se, populations selfed one generation, and population crosses for three methods of recurrent selection conducted in Iowa Stiff Stalk Synthetic (BSSS). Adapted from Helms (1986).

Populations and crosses†	Lodging							
	Yield		Grain moisture		Root		Stalk	
	Per se	Self	Per se	Self	Per se	Self	Per se	Self
	— Mg ha ⁻¹ —				%			
BSSSC0	3.85	2.51	27.6	27.8	15.7	16.0	31.0	24.6
BS13(HT)C2	4.31	2.65	27.6	27.8	20.6	15.5	27.2	24.7
BS13(HT)C4	4.64	2.91	27.1	28.7	17.9	18.4	33.1	22.6
BS13(HT)C6	4.98	3.23	28.4	29.0	30.9	24.2	25.8	19.2
BS13C0	5.27	3.37	28.6	28.7	28.8	26.6	18.7	19.1
BS13(S)C2	5.22	3.91	26.8	27.3	14.4	15.1	32.7	26.7
BS13(S)C4	5.32	4.10	25.9	26.5	15.7	19.4	30.0	29.0
‡	38.2	63.3	-6.2	-4.7	0.0	21.2	-3.2	17.9
BSSS(R)C2	4.51	2.69	25.2	25.6	17.6	15.2	33.3	24.7
BSSS(R)C4	4.56	2.76	24.7	24.7	17.9	16.4	22.4	25.4
BSSS(R)C6	5.27	3.03	27.0	27.8	16.0	14.4	20.3	20.2
BSSS(R)C8	5.09	3.06	25.8	27.1	19.7	16.9	16.4	17.2
BSSS(R)C10	5.31	3.66	26.5	27.5	16.0	12.9	16.6	19.4
‡	37.9	45.8	-4.0	-1.1	1.9	-19.4	-46.5	-21.1
BSSSC0 × BSCB1C0	5.13	--	23.7	--	16.8	-	32.9	--
BSSS(R)C6 × BSCB1(R)C6	6.38	--	25.3	--	16.6	--	23.1	--
BSSS(R)C10 × BSCB1(R)C10	7.30	--	24.5	--	13.7	--	17.6	--
§	42.3		3.4		-18.5		-46.5	
BS13(S)C4 × BSSS(R)C10	7.32	--	26.2	--	19.6	-	21.9	--
BS13(S)C4 × BSCB1(R)C10	7.45	--	23.7	--	16.7	--	21.5	--
B84 × Mo17	9.48	--	25.0	--	14.7	--	16.8	--
B73 × Mo17	8.55	--	25.5	--	12.3	--	15.3	--
LSD (0.05)	0.5		1.3		6.5		7.9	

† BSSSC0 is the original strain of Iowa Stiff Stalk Synthetic; HT populations derived from BSSSC0 half-sib family selection using Ia13 as tester; S populations derived by inbred progeny selection, which was initiated in BS13(HT)C7; R populations derived from BSSSC0 by reciprocal recurrent selection with BSCB1 as the tester.

‡ Percentage change for last cycle of selection relative to BSSSC0.

§ Percentage change of cross relative to BSSSC0 × BSCB1C0.

(36.0%) was similar but reduced to 22.9% for BS13(S)C4. Average estimate of inbreeding for C6 and C8 of BSSS(R) was 41.2%, which is 5.2% greater than BS13(S)C0 [or BS13(HT)C7].

Fifty S₂ progenies derived from BSSSC0 and four selected populations were evaluated in six environments to estimate the genetic variability of the respective populations (Table 8-17). Except for grain yield of BSSS(R)C9 developed by nine cycles of reciprocal recurrent selection, the estimates of genetic variability among S₂ progenies do not suggest a significant change from BSSSC0. Average yield of S₂ progenies for each

Table 8-17. Means and estimates of genetic variance (σ^2_g) for five traits for 50 S_2 progenies derived from BSSSC0 by recurrent selection evaluated in six environments. Adapted from Helms (1986).

Populations†	Grain			Moisture			Root			Lodging		
	Yield		$\sigma^2_{\bar{x}}$			$\sigma^2_{\bar{x}}$			$\sigma^2_{\bar{x}}$			$\sigma^2_{\bar{x}}$
	$\bar{x}$			$\bar{x}$			$\bar{x}$			$\bar{x}$		
	Mg ha ⁻¹ †						%					
BSSSC0	2.12	41.0 ± 9.8		26.5	4.7 ± 1.2		16	59 ± 17		15	78 ± 19	
BSSS(R)C5	2.62**	58.4 ± 13.4		25.4**	4.4 ± 1.0		18	53 ± 15		15	61 ± 15	
BSSS(R)C9	3.40**	15.5 ± 5.0		26.0*	2.8 ± 0.7		17	62 ± 17		11**	31 ± 8	
BS13(S)C0	3.32**	32.1 ± 8.0		26.1*	4.5 ± 1.1		25**	185 ± 46		10**	50 ± 13	
BS13(S)C3	3.84**	44.1 ± 11.5		24.9**	3.7 ± 0.9		20**	65 ± 20		16	100 ± 25	
LSD (0.05)	0.12			0.4			2.1			1.5		
LSD (0.01)	0.15			0.5			2.8			1.9		

** Significantly different from BSSSC0 at the 0.05 and 0.01 levels, respectively.
† BSSSC0 is the original strain of Iowa Stiff Stalk Synthetic; R populations obtained by reciprocal recurrent selection with BSCB1 as the tester; BS13(S)C0 was obtained after seven cycles of half-sib selection with double-cross hybrid Ia13 as the tester; and BS13(S)C3 developed after three cycles of inbred progeny selection where BS13(S)C0 is equivalent to BS13(HT)C7.
‡ Mg ha⁻¹ × 10².

population (Table 8-17) exhibited trends similar to those for the S₁ generation presented in Table 8-16. Inbreeding depression of S₂ progenies derived from populations after selection was reduced in all instances. Also, the average yields of S₂ progenies derived by half-sib family selection [BSSS(R)C9 and BS13(S)C0 or BS13(HT)C7] were similar (3.40 vs. 3.32 Mg ha⁻¹). The BS13(S)C3 S₂ progenies averaged 81.1% greater yield than the BSSSC0 S₂ progenies, or 8.1% increase cycle⁻¹ of selection.

Grain yield was the primary trait in selection, and the response to selection was consistent over cycles of selection (3.8% cycle⁻¹) for the populations themselves. Grain moisture is a measure of maturity, and, in most instances, the grain moisture of the selected populations was significantly less than BSSSC0 (Tables 8-16 and 8-17). Although attention was given to root and stalk quality during selection, trends for improved root and stalk quality were not evident for either the populations or the inbred populations.

Estimates of the genetic parameters for the Smith (1983) model were obtained for both methods of selection for grain yield (Table 8-18). Changes in frequencies of alleles with additive effects (ALI) due to selection were greater in the BS13(HT) and BS13(S) than in BSSS(R). But the changes in frequencies of alleles with dominance effects (DLI) were more important in BSSS(R) than in the BS13(HT) and BS13(S) populations over cycles of selection. Significant estimates of genetic drift (DQI) over cycles of selection for grain yield were similar for BS13(HT) and BSSS(R); Smith (1979a) reported greater inbreeding depression for the BSSS(R) method, although the effective population size was the same for both methods. The estimate of genetic drift in BS13(S) was smaller and nonsignificant. Based on the estimates of the effects of genetic drift, yield of the populations was adjusted for genetic drift (Table 8-18). The observed yields for BSSS(R)C6 and BS13(HT)C7 were equal, but the ad-

Table 8-18. Estimates of genetic parameters and observed and predicted grain yield in selected populations of BSSS. Adapted from Helms (1986).

Populations	Genetic parameters for yield†			Grain yield		
	ALI	DLI	DQI	Populations	Observed	Predicted
		Mg ha ⁻¹			Mg ha ⁻¹	
BS13(HT)C7	0.090**	0.082*	-0.013**	BSSSC0‡	3.85	3.93
BS13(S)C4	0.113**	--	-0.019	BS13(HT)C7	5.27	6.34
BSSS(R)C10	0.047	0.131**	-0.012**	BS13(S)C4	5.32	7.24
				BSSS(R)C6	5.27	6.06
				BSSS(R)C10	5.31	7.49

† Genetic parameters based on model used by Smith (1983) where ALI, DLI, and DQI are partial regression coefficients due to the effects of homozygous loci, heterozygous loci, and genetic drift, respectively, on cycles of selection.

‡ BSSSC0 is the original strain of Iowa Stiff Stalk Synthetic; BS13(HT)C7 after seven cycles of half-sib family selection with Ia13 tester; BS13(S)C4 after four cycles of inbred progeny selection in BS13(HT)C7; and BSSS(R) after reciprocal recurrent selection with BSCB1 as the tester.

justed yields show that seven cycles of half-sib family selection with Ia13 was 4.5% greater than six cycles of reciprocal recurrent selection. BSSS(R)C10 was only 3.4% greater than BS13(S)C4. Total response, both observed and adjusted for genetic drift, was similar for the advanced populations of BSSS.

8-2.3.1.5 Full-sib Family Selection. One of the first recurrent selection programs used in corn was full-sib family selection within 'Jarvis' and 'Indian Chief' (Moll and Robinson, 1966). This selection program was started in the late 1940s and has continued to the present time. Periodic reports of response to selection, both direct and indirect, usually involved comparisons with reciprocal half-sib recurrent selection conducted in the same populations. Populations per se and population crosses of the respective recurrent selection programs have been evaluated to measure direct and indirect responses realized from intra- and interpopulation recurrent selection. Grain yield was the trait of selection.

Moll and Hanson (1984) reported grain yield data for two experiments (Exp. 1 and 2) that included the direct response in the Jarvis and Indian Chief populations themselves and the correlated response of their population crosses (Table 8-19). Data were available for 10 cycles of full-sib family selection. Response to selection for greater grain yield was more effective in Jarvis than in Indian Chief in both experiments. Though yields in Exp. 2 were greater than in Exp. 1, similar responses were obtained. Response seemed to have plateaued after the C8, and Moll and Hanson (1984) combined the data for C8 and C10. For the average of the two experiments, grain yield increased 2.62% cycle⁻¹ for Jarvis and 0.65% cycle⁻¹ for Indian Chief. Moll and Hanson (1984) also reported data for ear number, and, in both experiments, the increase in ear number was at a lower rate in Indian Chief ($b = 0.031$ ears cycle⁻¹) than in Jarvis ($b = 0.0565$ ears cycle⁻¹).

Crosses between the Jarvis and Indian Chief populations developed

Table 8-19. Responses for grain yield after 10 cycles of full-sib family selection in Jarvis and Indian Chief. Adapted from Moll and Hanson (1984).

Cycles of selection	Jarvis		Indian Chief		Jarvis × Indian Chief	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2
	Mg ha ⁻¹					
C0	5.02	7.36	5.77	8.54	6.22	8.93
C4	5.69	--	5.67	--	6.85	--
C8	6.79	9.03	6.48	8.49	7.45	10.77
C10	6.57	8.85	6.41	8.92	7.35	11.18
C8 and C10‡	--†	8.94	--†	8.70	--†	10.98
b, Mg ha ⁻¹ cycle ⁻¹	0.176	0.166	0.081	0.025	0.122	0.226
Change, %§	30.9	21.5	11.1	1.9	18.2	23.0

† Data were not available.

§ Change relative to C10 or C8 and C10.

‡ Data from C8 and C10 were combined.

by full-sib family selection were evaluated in the same experiments. Responses in the population crosses were similar to those for Jarvis; 2.06% cycle⁻¹ for crosses vs. 2.62% for Jarvis (Table 8-19). Midparent heterosis increased from 13.5% in the C0 crosses to 19.7% in the C10 crosses. Response to selection in Jarvis was reflected in the population crosses. The differences in response to full-sib family selection in Jarvis and Indian Chief were discussed by Moll and Hanson (1984) relative to genetic divergence, effective population size, and number of ears plant⁻¹. It seems the effectiveness of full-sib family selection also was related to the initial yield levels and number of ears plant⁻¹ in Jarvis and Indian Chief. The Indian Chief C0 had 15.6% greater yield (Table 8-19) and 34% greater ear number than the Jarvis C0 (Moll and Hanson, 1984). After 10 cycles of full-sib family selection, Jarvis was 2.6% greater yielding than Indian Chief but had fewer ears per plant than Indian Chief (1.63 for Indian Chief vs. 1.54 for Jarvis). Number of ears increased 54.5% with 10 cycles of full-sib family selection for grain yield in Jarvis and 21.6% in Indian Chief. Full-sib family selection was effective for increasing number of ears, an important component of yield, in Jarvis. Hence, a portion of the difference in response of Jarvis and Indian Chief to full-sib family selection may be due to the initial yield level in Indian Chief, enhanced by a greater frequency of ears per plant.

Full-sib family selection also has been used extensively by breeders at CIMMYT (1982). One of the problems encountered in the breeding and selection of tropical corn has been the tall, leafy nature of the plant, and, consequently, a low grain-to-stover ratio (harvest index). A selection study was initiated within and among full-sib families of 'Tuxpeno Crema 1' to improve its harvest index. Twenty cycles of selection increased the harvest index from 0.30 to 0.49, which is similar to U.S. Corn Belt materials (Table 8-20). Correlated changes with selection for an improved harvest index included 47.6% decreased plant height, 67.6% greater grain yield, and 9% less total dry matter. Full-sib family selection, therefore, was effective for improving the primary trait (harvest index), associated

Table 8-20. Response to within and among full-sib family recurrent selection for reduced plant height in Tuxpeño Crema 1. Adapted from CIMMYT (1982).

Cycles of selection	Plant ht.	Grain yield	Total dry matter	Harvest index
	cm	Mg ha ⁻¹		
0	273	4.05	14.94	0.30
6	211	5.54	14.75	0.38
9	203	5.67	15.32	0.39
12	196	6.18	15.37	0.41
15	173	6.73	15.12	0.46
17	156	6.23	13.10	0.47
20	143	6.79	13.60	0.49
bl	-6.1 ± 0.5	0.12 ± 0.02	-0.07 ± 0.05	0.020 ± 0.005
Change, %	-47.6	67.7	-9.0	63.3

with changes in the desired direction for the other traits. Because harvest index is a ratio of grain to total dry matter, the correlated changes would be expected to provide an increase in the harvest index; greater grain yield and less total dry matter, which can be achieved by reducing plant stature. An index, therefore, rather than a single trait was used in selection. Johnson et al. (1986) evaluated the same population after 15 cycles of selection. Selection resulted in a linear reduction of 2.4% cycle⁻¹ in plant height from 282 to 179 cm. With the reduction in plant height, optimum plant density increased from 48 000 to 64 000 plants ha⁻¹, and yield increased 2.1% cycle⁻¹. Yield improvement was correlated with a linear increase in harvest index from 0.30 for the C0 to 0.45 for the C15.

Full-sib family selection also has been used at CIMMYT (1984) to increase grain yield (Table 8-21). Data from evaluation trials after four and five cycles of full-sib family selection in eight tropical populations showed an average yield increase of 5.9 or 1.3% cycle⁻¹ (Pandey et al., 1986). Response to selection, however, varied among populations, ranging from 0.2% cycle⁻¹ for 'Tuxpeno Caribe' to 9.5% for 'Cogollero' and 9.1% for 'Amarillo Cristalino-1'. Rate of response to selection was related to the original yield level of the populations. Yield of Amarillo Cristalino-1 C5 was 5.27 Mg ha⁻¹ (9.1% increase) vs. Tuxpeno Caribe C5, which yielded 6.21 Mg ha⁻¹ (0.2% increase). A more favorable comparison was for the 'La Posta' population because yield increased from 6.12 Mg ha⁻¹ for the C0 to 6.58 Mg ha⁻¹ for the C4, a 7.5% yield increase at a greater yield level. On the average, full-sib family selection was effective in reducing the days-to-silk (-0.6% cycle⁻¹), plant (-1.1% cycle⁻¹) and ear (-1.8% cycle⁻¹) height, and increasing number of ears plant⁻¹ (0.9% cycle⁻¹).

Singh et al. (1986) effectively used full-sib family selection to increase the level of prolificacy in the open-pollinated cv. Partap. Selection was practiced at two plant densities of 44 444 and 166 666 plants ha⁻¹. Linear response per cycle for number of ears per plant was significant at both densities, but the response at the lower density (0.06 ears or 5.5%) was

Table 8-21. Average response to full-sib family selection for grain yield, days-to-silk, and plant height for eight tropical populations. Adapted from CIMMYT (1984).

Cycles of selection	Traits		
	Grain yield	Days-to-silk	Plant ht.
	Mg ha ⁻¹	no.	cm
C0	5.88	67.2	229.2
C4-C5†	6.23	65.4	218.4
Response, %	5.93	-2.6	-4.6
Range, %	0.16-9.46	-4.4-1.4	-9.0-3.8
Response cycle ⁻¹ , %	1.27	-0.6	-1.0
Range, %	0.03-1.89	-0.9-0.3	-1.9-0.8

† Four cycles of selection completed in three populations and five cycles completed in five populations.

greater than at the higher density (0.04 ears or 3.6%). A significant correlated increase of $4.5\% \text{ cycle}^{-1}$ in grain yield was obtained. Although there were some differences in correlated responses at the two plant densities, Singh et al. (1986) concluded full-sib family selection may be effective in developing higher-yielding, earlier-maturing, and shorter-statured genotypes.

Full-sib family selection has not been used as extensively as half-sib family or inbred progeny selection. In certain situations, full-sib family selection is effective and appropriate. In some situations (e.g., international testing), full-sib family selection is useful to provide an adequate amount of seed for testing, relative ease in producing the seeds, and progeny vigor where vigor is important to establish stands and compete with other plants. Full-sib selection has been used effectively for developing improved CIMMYT corn populations and providing flexibility in the types of cultivars that can be used in national programs; i.e., improved populations, improved full-sib families, hybrids, and extraction of inbred lines (Pandey et al., 1986).

8-2.3.2 Interpopulation Selection

Because of the importance of the phenomenon of heterosis in hybrid corn, selection methods that emphasize cross performance are of interest. Interpopulation selection methods arose from the opposing advocates of the relative importance of overdominance vs. partial-to-complete dominance of loci acting in an additive manner as the genetic basis for heterosis. Definitive evidence supporting the opposing views was not available. Thus, Comstock et al. (1949) developed reciprocal recurrent selection to permit selection of both types of genetic effects in selection among half-sib family crosses produced between two populations. From theoretical considerations, Comstock et al. (1949) concluded that under no conditions would reciprocal recurrent selection be more than slightly inferior to selection methods that emphasized selection for either specific (Hull, 1945) or general combining ability (Jenkins, 1940). Direct response for interpopulation selection methods is, therefore, measured in the population crosses, and indirect response is determined from the populations themselves. The populations for the cycles of selection are formed by intermating progenies that had superior performance in crosses with the opposing population; i.e., the opposing advanced populations are the respective testers.

Yield has been the primary trait of selection for the interpopulation selection methods. Because of the complexity for developing progenies and the greater heritability of other traits considered for selection, interpopulation selection methods have not been considered in selection for maturity, pest resistance, stalk quality, plant stature, prolificacy, and cold tolerance. Consequently, the number of interpopulation selection studies is less than for intrapopulation selection.

8-2.3.2.1 Reciprocal Recurrent Selection. Reciprocal recurrent se-

lection was the original method suggested by Comstock et al. (1949), and it has received greatest attention in corn breeding. The method includes two genetically broad-based populations (e.g., A and B) with good performance that are of interest to breeding programs. Two sets of half-sib families are produced and evaluated. Plants in a population A are selfed and crossed to a sample of plants from B. Similarly, plants in population B are selfed and crossed to a sample of plants from A. Both sets of half-sib families are evaluated in replicated trials repeated over environments. S_1 progenies of S_0 plants having superior testcross performance are intermated to form the next cycle of selection. Cycles of selection are repeated using the latest cycle populations to produce the testcrosses. Except for the modifications suggested by Paterniani (1978) and Paterniani and Vencovsky (1977) the mechanics of conducting reciprocal recurrent selection are the same as those described by Comstock et al. (1949).

Reciprocal recurrent selection programs were initiated to test the method, and the two programs that have had the longest selection history include Jarvis and Indian Chief and Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic #1 (BSCB1). Jarvis and Indian Chief are open-pollinated cultivars whereas BSSS and BSCB1 are synthetic cultivars formed by intermating 16 (BSSS) and 12 (BSCB1) selected lines. Data from both programs have been reported on a regular basis during the course of selection, and only a brief summary of the data available will be included.

Moll and Hanson (1984) reported progress following 10 cycles of reciprocal recurrent selection in Jarvis and Indian Chief for grain yield and number of ears (Table 8–22). The selection criterion was yield of ear corn, and care was taken to avoid selection for any other trait. Data from two experiments were available to estimate direct response in the population crosses. Although the yield difference between the two experiments was 1.70 Mg ha^{-1} , the estimates of linear regression coefficients (0.153 and $0.202 \text{ Mg ha}^{-1} \text{ cycle}^{-1}$) and percentages of response (19.8 and 20.9%) following selection were similar. Direct response, therefore, was about $2\% \text{ cycle}^{-1}$ of selection. Correlated responses in Jarvis and Indian Chief were different, but consistent for the two experiments. Average response in Jarvis was $0.160 \text{ Mg ha}^{-1} \text{ cycle}^{-1}$, whereas a negative response of $-0.078 \text{ Mg ha}^{-1} \text{ cycle}^{-1}$ was realized in Indian Chief. Indian Chief C0 was 15.6% greater yielding than Jarvis C0, but following 10 cycles of reciprocal recurrent selection Jarvis C10 was 18.8% greater yielding than Indian Chief C10. Relative yields of the two populations were nearly equal at the C4. The 24.4% yield increase in Jarvis paralleled the 20.4% yield increase in the population cross. Midparent heterosis increased from 13.8% for the C0 population cross to 28.9% for the C10 population cross. High-parent heterosis also increased from 6.2 to 18.7%, but there was a reversal in the high parent.

Moll and Hanson (1984) also noted a change in response at the C8, which suggested selection reached a plateau following the eighth selection

Table 8-22. Grain yield and ear number response after 10 cycles of reciprocal recurrent selection in Jarvis and Indian Chief. Adapted from Moll and Hanson (1984).

Cycles of selection	Yield			Ear plant ⁻¹		
	Jarvis	Indian Chief	Jarvis by Indian Chief	Jarvis	Indian Chief	Jarvis by Indian Chief
	Mg ha ⁻¹			no.		
Experiment 1						
C0	5.02	5.77	6.22	0.99	1.30	1.25
C4	5.49	5.57	6.48	1.23	1.41	1.37
C8	6.59	5.43	7.77	1.54	1.46	1.56
C10	6.36	5.36	7.45	1.63	1.55	1.66
b†	0.157	-0.041	0.153	0.066	0.023	0.041
Response, %‡	26.7	-7.1	19.8	64.6	19.2	32.8
Experiment 2						
C0	7.36	8.54	8.93	1.01	1.38	1.29
C8	9.31	7.76	10.77	1.63	1.50	1.75
C10	8.66	7.34	10.84	1.68	1.73	1.83
C8 + C10	8.98	7.55	10.80	1.66	1.62	1.79
b†	0.162	-0.114	0.202	0.070	0.029	0.055
Response, %‡	22.0	-11.6	20.9	64.4	17.4	38.9

† b = regression coefficient with Mg ha⁻¹ cycle⁻¹ for yield and number of ears plant⁻¹ cycle⁻¹ for ear number.

‡ Change in mean for last cycle of selection relative to the C0.

cycle. They explored several reasons for the possible plateau, including divergence, inbreeding depression, environmental effects, and changes in ears per plant (Table 8-22). Full-sib selection (Table 8-16) caused divergence for additive effects, whereas reciprocal recurrent selection utilized additive effects of Jarvis and dominance effects from Indian Chief. The changes in response between the C8 and C10 occurred when differences involving dominance occurred. This change may be related to the unique environments available for testing, but the changes occurred for both the full-sib and reciprocal recurrent selection methods, which were conducted in alternate years. Thus, the environmental effects did not seem to be a plausible explanation. Inbreeding depression did not seem reasonable because population crosses as well as the populations per se, had a similar trend. Ears plant⁻¹ have been shown to be associated with greater yields. Ears plant⁻¹ increased 64.5% in Jarvis and 18.3% in Indian Chief, but by the C8 ear number was similar for both populations (Table 8-22). Hence, they hypothesized that genetic adjustments may be required for the greater sink capacity of prolific plants. They concluded, however, that the lack of response may be transitory, and that future selection may cause changes different from those experienced following 10 cycles of selection.

Smith (1983, 1984) presented a detailed analysis following seven cycles of reciprocal recurrent selection in BSSS and BSCB1. Preliminary data for different cycles of selection and Smith's (1983, 1984) data for

grain yield are summarized in Table 8-23. Grain yield was the primary trait of selection, but there was also selection for European corn borer resistance, root and stalk quality, and maturity. At the C5, individual S₁ plants from selected S₁ progenies were used to produce the half-sib families, and all evaluation trials were machine planted and harvested. Also,

Table 8-23. Grain yield response of populations per se and after one generation fo self-ing following reciprocal recurrent selection in BSSS and BSCB1 and their crosses and half-sib family and inbred progeny selection in BS13 and crosses with BSSS(R) and BSCB1(R).

Cycles of selection	Smith (1983)		Martin & Hallauer (1980)	Tanner (1984)	Smith (1984)	Helms (1986)	
	Per se	Selfed	Per se	Per se	Per se	Per se	Selfed
Mg ha ⁻¹							
BSSSC0	5.97†	3.53†	5.00†	4.81†	--	3.85†	2.51
BSSS(R)C4	6.24	3.84	5.32	--	6.43†	4.56	2.76
BSSS(R)C7	6.89	4.23	5.24	5.89§	7.11§	5.18¶	3.04¶
BSSS(R)C10	--‡	--	--	--	--	5.31	3.66
Response, %	15.4	19.8	4.8	22.4	37.9	45.8	
BSCB1C0	5.34	3.64	5.18	4.73	--	--	--
BSCB1(R)C4	5.52	3.38	5.18	--	5.68	--	--
BSCB1(R)C7	5.61	3.16	4.74	3.70†	5.10	--	--
Response, %	5.1	-13.2	-9.5	-21.8	--	--	--
BSSSC0							
× BSCB1C0	7.31	4.16	5.85	5.94	--	5.13	--
BSSS(R)C4							
× BSCB1(R)C4	7.90	3.60	6.74	--	8.60	--	--
BSSS(R)C7							
× BSCB1(R)C7	9.13	4.95	7.07	8.34	9.08	6.38#	--
BSSS(R)C10							
× BSCB1(R)C10	--	--	--	--	--	7.30	--
Response, %	24.9	19.0	20.8	40.4	--	42.3	--
BS13(HT)							
× BSSSC0	6.62	4.67	--	--	--	5.39	--
BS13(HT)C7							
× BSSS(R)C7	8.53	5.57	--	--	--	6.49	--
BS13(HT)C7							
× BSCB1C0	7.33	4.84	--	--	--	--	--
BS13(HT)C7							
BSCB1(R)C7	9.00	4.46	--	--	--	6.89	--
BS13(S)C4							
× BSSS(R)C10	--	--	--	--	--	7.32	--
BS13(S)C4							
× BSCB1(R)C10	--	--	--	--	--	7.45	--
LSD (0.05)	0.588	0.588	0.532	0.656	0.590	0.469	0.469

† Each data point is an average of 20 observations for Smith (1983), 30 observations for Martin and Hallauer (1980), 16 observations for Tanner and Smith (1987), 20 observations for Smith (1984), and 30 observations for Helms (1986).

‡ No data were obtained.

§ Data were obtained in C8 by Tanner and Smith (1987) and Smith (1984).

¶ Data were averaged for C6 and C8 by Helms (1986).

Data were for C6 by Helms (1986).

during the cycles of selection, changes were made in plant densities, amounts of fertilizer applied, types of herbicides applied, and field husbandry in seedbed preparation. A selection index that included grain yield, stand, lodging, and grain moisture was used to make selections in later cycles (Smith et al., 1981a, b). Hence, the definition of grain yield has changed with cycles of selection, and the emphasis in selection for other traits also has changed during the cycles of selection. Another important contrast in comparison with Jarvis and Indian Chief is that only 10 rather than 20, superior S_1 progenies were intermated to form the next cycle population.

Direct response for grain yield has been consistent and positive in all evaluations, ranging from 3 to 4% cycle⁻¹ of selection. Indirect response in the populations themselves follows a trend similar to that reported in Jarvis and Indian Chief; BSSS responded to selection (2–3% cycle⁻¹) whereas BSCB1 did not significantly change (Smith, 1983) or had a significant decrease (Tanner and Smith, 1987). Because of the changes in experimental procedures, Smith (1983) estimated the progress for two intervals (C0–C4 and C4–C8) of selection. Improvements in grain yield for the crosses were $0.247 \pm 0.033 \text{ Mg ha}^{-1}\text{cycle}^{-1}$ for cycles C0–C4 and $0.361 \pm 0.045 \text{ Mg ha}^{-1}\text{cycle}^{-1}$ for cycles C4–C8. The difference in rate of cross improvement ($0.115 \pm 0.068 \text{ Mg ha}^{-1}$) was significant, suggesting that machine harvesting and use of S_1 plants in making testcrosses increased response to selection. The observed response, averaged over all cycles, was 4.7% cycle⁻¹ or 1.4% yr⁻¹ assuming 3 yr cycle⁻¹.

Smith (1983) also included crosses of BS13(HT) with BSSS(R) and BSCB1(R). Gain for grain yield of BS13(HT) $\times$ BSCB1(R) was estimated as $0.229 \pm 0.020 \text{ Mg ha}^{-1}\text{cycle}^{-1}$, and the differences for the two intervals were not significant. This estimate is similar to $0.231 \pm 0.037 \text{ Mg ha}^{-1}\text{cycle}^{-1}$ following five cycles reported by Eberhart et al. (1973). Though BS13(HT) was developed with use of the Ia13 double cross as tester, the response to selection was similar with BSCB1(R). Crosses between the two selected strains of BSSS, BS13(HT), and BSSS(R), were estimated to be $0.219 \pm 0.031 \text{ Mg ha}^{-1}\text{cycle}^{-1}$ for cycles 0–4 and $0.586 \pm 0.069 \text{ Mg ha}^{-1}\text{cycle}^{-1}$ for cycles 4–7. The cross of BS13(HT)C7 $\times$ BSSS(R)C7 yielded 8.53 Mg ha^{-1} vs. 5.97 Mg ha^{-1} for BSSSC0. Similar responses of crosses between BSSS strains were reported by Russell and Eberhart (1975), Stangland et al. (1982), and Oyervides and Hallauer (1986). Smith (1983) also estimated a parameter, DQI, which is a measure of the loss of heterozygotes in the population per se. He estimated DQI to be $-0.036 \pm 0.004 \text{ Mg ha}^{-1}$ in BSCB1(R), $-0.022 \pm 0.003 \text{ Mg ha}^{-1}$ in BSSS(R), and $-0.013 \pm 0.003 \text{ Mg ha}^{-1}$ in BS13(HT). The lack of response in the populations themselves could be due to the loss of heterozygotes due to drift and selection. Because only 10 progenies were recombined between cycles of selection, the effects of drift could be important. Helms (1986) also obtained a significant estimate for the loss of heterozygotes due to drift in BSSS(R) and BSCB1(R).

Other plant and ear trait data have been obtained in the evaluations of BSSS(R) and BSCB1(R). In most instances, the trends, though not generally statistically significant, are in the desirable direction: decrease in ear height, decrease in stalk lodging with no change in root lodging, greater number of ears, 1% increase in grain moisture at harvest, and an increase in ear length and kernel weight. These changes occurred in both the populations themselves and population crosses. Days to flowering decreased in BSSS(R) and the population crosses but increased in BSCB1(R). Because BSSSC0 was 5 to 7 d later flowering than BSCB1C0, the changes in flowering were a result of selection in producing the half-sib families.

Reciprocal recurrent selection has been shown to be effective for improvement of the population crosses for the limited number of studies conducted. Indirect responses in the populations themselves have not been as consistent (Martin and Hallauer, 1980). Except for the studies involving Jarvis and Indian Chief and BSSS and BSCB1 the number of cycles of selection have not been adequate to determine the long-term effects of reciprocal recurrent selection (Collier, 1959; Gevers, 1975; Darrah et al., 1978; Paterniani and Vencovsky, 1977). It would be desirable if further information were available for population types, effective population sizes, and different environments tested to determine the utility of reciprocal recurrent selection for applied corn breeding programs.

8-2.3.2.2 Reciprocal Full-sib Selection. The principles of reciprocal full-sib selection are similar to those for reciprocal recurrent selection. The one basic difference is that full-sib families rather than half-sib families are produced for evaluation. Rather than producing reciprocal testcrosses of individual plants in one population with a sampling of individuals from the other population, reciprocal crosses (full-sib families) between individual plants are evaluated. The most effective method is to include two populations that have a strong two-ear expression (Hallauer and Eberhart, 1970). Full-sib families are produced by making reciprocal crosses between plants (one from population A and one from population B) on one ear of each plant and selfed seed is produced on the other ear. Full-sib families are evaluated, and S_1 progenies of the superior families are recombined for the respective populations. Direct selection is for the population crosses and indirect selection is for the populations themselves, which is the same as for reciprocal recurrent selection. One other suggested advantage of reciprocal full-sib selection is that the method is directly applicable for development of single crosses (Hallauer, 1967, 1973; Lonnquist and Williams, 1967).

The most extensive data available for reciprocal full-sib selection are those for 'Iowa Two-ear Synthetic' (BS10) and 'Pioneer Two-ear Composite' (BS11) following seven cycles of selection (Hallauer, 1984). Direct response for grain yield was $2.1\% \text{ cycle}^{-1}$ in the population cross; indirect response was $2.7\% \text{ cycle}^{-1}$ for BS10 and $2.4\% \text{ cycle}^{-1}$ for BS11. Heterosis increased over cycles of selection from 6.3% for the C0 population cross

to 28.4% for the C7 population cross. Heritability of full-sib families averaged 61% over cycles of selection with no evidence that the variability among full-sib families had decreased from the C0 ($\sigma_G^2 = 3.53 \pm 0.50$) to the C7 (3.33 ± 0.62). Six hybrid checks were included with the full-sib families in the evaluation trials for each cycle of selection. Relative to the mean of the six hybrid checks, the mean of the full-sib families was changed from three deviations below the mean of hybrid checks to three standard deviations above the mean of the hybrid checks (Fig 8–8). Grain yield was emphasized in selection, but attention also was given to maturity and standability. Relative to the common check hybrids, the changes, although not significant in all instances, have been in the desired direction (Hallauer, 1984).

Reciprocal full-sib selection has been effective for improvement of BS10, BS11, and the population cross. Rate of response to selection was similar to the other intra- and interpopulation selection methods. Originally, the method was designed to maximize selection for specific combining ability with use of prolific plants to produce the full-sib families and S_1 progenies. Prolific plants, however, are not a prerequisite for use of reciprocal full-sib selection (Hallauer, 1973). Full-sib families can be obtained by use of S_1 progenies. Marquez-Sanchez (1982) also has suggested modifications of reciprocal full-sib selection that do not require

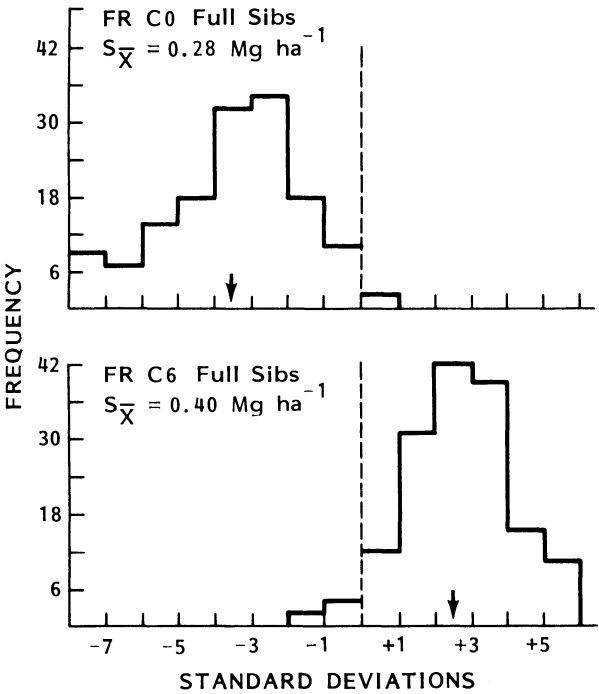


Fig. 8–8. Grain yield distribution of the C0 and C6 full-sib families relative to the mean of the six check hybrids. Arrows indicate means of the full-sib families and dashed lines indicate means of six check hybrids. Adapted from Hallauer (1984).

prolificacy and reduce the rate of inbreeding. Use of S_1 progenies requires an additional generation, but the effectiveness of selection among and within S_1 progenies may compensate for the additional generation; Smith (1983) suggested that use of S_1 progenies contributed to the continued improvement of reciprocal recurrent selection. Though specific combining ability between pairs of genotypes is emphasized, Hoegemeyer and Hallauer (1976) reported that in crosses among elite lines selected by reciprocal full-sib selection general combining ability was of greater importance than specific combining ability. Significant specific combining ability effects were more frequent among crosses selected by reciprocal full-sib selection and were of greater magnitude than among crosses of unselected lines. But the elite lines selected within pairs of genotypes also had good general combining ability with other elite lines. These results for reciprocal full-sib selection agree with the results Horner (1985) reported with recurrent selection using an inbred tester.

It seems, so far, that additive genetic effects with partial to complete dominance are of greater importance and most methods seem to respond to selection for these effects. Some methods of selection (e.g., inbred progeny) may be more effective than others, but the comparisons do not permit definite discrimination among selection methods. The results noted by Moll and Hanson (1984) following 10 cycles of reciprocal recurrent selection in Jarvis and Indian Chief may be a reflection of the genetic adjustments being made for different types of genetic effects. Hoegemeyer and Hallauer's (1976) data were derived for the C_0 . Different effects may be of greater importance if the single crosses were derived following 10 cycles of reciprocal full-sib selection. Comparisons of responses to selection, either direct or indirect, between reciprocal full-sib selection and other selection methods are limited.

Jones et al. (1971) compared reciprocal recurrent selection based on either half-sib or full-sib family selection algebraically and with computer simulation. The relative performance of the two methods depended on selection intensity and the environmental variance. Reciprocal full-sib selection was superior to reciprocal half-sib selection at less intense selection and when the environmental variance was large relative to the genetic variance. An example from some empirical estimates of variability among half-sib and full-sib families suggested that the selection differential should be 1.2 times greater for full-sib than for half-sib family selection to give similar response. The simulation studies indicated that full-sib family selection tended to give greater response in the mean of the population cross than half-sib family selection for the genetic models considered. For a genetic model that assumed complete dominance, gene frequencies of 0.5, and no linkage, full-sib family selection gave greater response than half-sib family selection in the population cross throughout 20 cycles of selection; the superiority of full-sib family selection increased as the number of cycles of selection increased. West et al. (1980) reported comparisons of S_1 progeny vs. reciprocal full-sib selection after two cycles

of selection within and among three populations. Response to S_1 progeny selection was greater than reciprocal full-sib selection in the populations that were selfed and random mated one generation. Direct response from S_1 progeny selection was greater, therefore, than the indirect effects of reciprocal full-sib selection. But the direct effects of reciprocal full-sib selection were equal to the indirect effects of S_1 progeny selection in the population crosses. Lantin and Hallauer (1981) compared 10 cycles of mass selection for prolificacy with five cycles of reciprocal full-sib selection for yield in BS10 and BS11. Reciprocal full-sib selection was more effective than mass selection for grain yield improvement and other agronomic traits. Both methods were equally effective for increasing number of ears plant⁻¹, but the correlated response of yield with increased ear number by mass selection was not effective. Because seed on two ears was required and yield was emphasized in reciprocal full-sib selection, there was a significant response for both traits.

8-2.3.3 Relative Response Among Methods

Comparisons of the relative effectiveness of different recurrent selection methods, and the types of genetic effects affected by selection are, in most instances, confounded by the different populations included in selection. Different methods were initiated at different times with different populations. Direct comparisons of relative effectiveness of reciprocal recurrent selection in BSSS and BSCB1 are not possible with reciprocal full-sib selection in BS10 and BS11 because of different genetic backgrounds of the two pairs of populations.

The differences that arise from different methods and different populations can be illustrated from the results reported for one method of selection conducted in different populations and different methods of selection in two common populations. Paliwal and Sprague (1981) reported gains following two or three cycles of full-sib family selection for improved yield within 13 populations. Gain cycle⁻¹ of selection ranged from 0.8 to 9.8%. The effectiveness of full-sib family selection obviously depended on the relative levels of grain yield and genetic variability of the populations, and, consequently, realized response to full-sib family selection. Average gain cycle⁻¹ of selection for the 13 populations was 3.4%, which is similar to the average gains reported by Sprague and Eberhart (1977) and Hallauer and Miranda (1981).

Darrah (1986) summarized gains from selection for yield improvement that included five (mass, ear-to-row, S_1 , half-sib, and full-sib) intrapopulation and three interpopulation methods of recurrent selection. Three populations were used: 'Kitale Synthetic II' (KSII) and 'Ecuador 573' (Ec573), which were shown to have good specific combining ability (Eberhart et al., 1967), and the population cross 'Kitale Composite A' (KCA). KCA was the base population for the intrapopulation methods that also included different levels of selection intensities for mass and ear-to-row selection methods. Grain yield was the primary trait in selec-

tion, and gains from selection were expressed on a per year basis. Averaged over selection variants, gains per year from selection in KCA were 2.3% for mass and 2.9% for ear-to-row selection for 10 cycles of selection. After five cycles of S_1 , half-sib, and full-sib selection, gains from selection were 0.9, 0.71 (average of three testers), and 3.6% yr^{-1} , respectively.

Ear-to-row, S_1 progeny, and reciprocal recurrent selection were conducted using the KSII and Ec573 populations. KSII did not respond to selection, whereas Ec573 responded to ear-to-row (4.6% yr^{-1} for 10 cycles) and S_1 progeny (3.5% yr^{-1} for five cycles) but not to reciprocal recurrent selection. Hence, only Ec573 had a direct response to ear-to-row and S_1 progeny selection, and neither population had an indirect response to reciprocal recurrent selection. Direct response in the population cross of KSII and Ec573 after five cycles of reciprocal recurrent selection was 2.8% yr^{-1} , but no response was realized in the population crosses following 10 cycles of ear-to-row and five cycles of S_1 progeny selection. Reciprocal recurrent selection was effective for improving the population cross, but it was not effective in the improvement of either KCII ($-0.005 \text{ Mg ha}^{-1}$) or Ec573 (0.066 Mg ha^{-1}). Responses to reciprocal recurrent selection were similar to those reported in other populations following five cycles of selection.

Although critical comparisons among methods of selection have not been available, the data reported by Paliwal and Sprague (1981) and Darrah (1986) suggest the rates of response, on the average, are similar among methods and among populations. Rates of response will vary among populations because of the genetic compositions of the populations (Paliwal and Sprague, 1981). But the rates of response among methods for the same populations also vary depending on how one measures the direct and indirect responses to selection.

8-2.3.4 Germ Plasm

Because genetic variability seems adequate in most populations for selection to be effective, the choice of population(s) to include for selection is important. It does not seem in most instances that adequate attention was given to the populations considered for selection. But this should not be considered a valid criticism for the populations used in past selection programs because comprehensive data were not available. BSSS and BSCB1 were included for reciprocal recurrent selection because BSSS had above average stalk quality and BSCB1 was developed by intermating inbred lines identified as having resistance to first-generation European corn borer. BS10 and BS11 were included for reciprocal full-sib selection because they both had a strong tendency for prolificacy. In neither instance, was there previous information relative to comparative mean performance with other possible populations, heterosis expressed in population crosses, inbreeding depression, total genetic variability, and data on other traits necessary for use of the populations improved by selection. Kitale Synthetic II and Ecuador 573 (Eberhart et al., 1967) and

BS10 and RSSC (Lambert, 1984) are exceptions because performance data were used to make the choice of populations to include for selection. Lonnquist and Gardner (1961) evaluated crosses of populations and how choice of population(s) can be made by performance per se and in crosses. Further information has been obtained in the past 20 yr on population performance, but data are not adequate or complete for the germplasm available to the breeders (Hallauer and Miranda, 1981). Ideally, the population(s) of choice would have performance traits that are acceptable for the target area and adequate genetic variability to permit effective selection. The only recourse is to survey populations available, glean information available, and consult with colleagues who have had experience with populations. Long-term nature of the recurrent selection methods requires a commitment for the populations chosen for selection.

8-2.4 Integration with Applied Breeding Programs

Recurrent selection methods should not be considered as separate entities from other aspects of productive applied breeding programs. If properly conducted, materials derived from recurrent selection programs can contribute to the other facets of programs dedicated to line and hybrid development (Eberhart et al., 1967). Genetic advance depends on conducting systematic selection programs that develop improved germ plasm sources for applied breeding programs. Systematic genetic improvement of germ plasm sources will contribute to realized genetic advance in the lines and hybrids extracted by conventional plant breeding methods.

Comparisons between recurrent selection techniques and pedigree selection methods were reported by Sprague (1952) and Duvick (1977). Sprague (1952) compared the increase in oil percentage of the corn kernel following five generations of pedigree selection and two cycles of recurrent selection. Depending on the comparison made, recurrent selection was 1.3 to 3.0 times more effective than pedigree selection. Duvick (1977) summarized data from four half-sib family recurrent selection programs and two pedigree selection experiments. Average rate of gain in grain yield yr^{-1} was 0.071 Mg ha^{-1} for recurrent selection and 0.068 Mg ha^{-1} for pedigree selection, assuming 3 yr to complete one cycle of recurrent selection and 13.3 yr to complete one cycle of pedigree selection. Duvick (1977) considered that rates of gain were essentially equal for the two systems, and that there was not an advantage in using one system compared with the other.

Recurrent and pedigree selection, however, should not be considered in opposition to one another. Rather, the two systems should complement each other. The goals of the two systems are different, but the ultimate objective is the same—contribute to genetic gain (Fig 8-4). The primary goal of recurrent selection is to develop improved sources of germ plasm that can be submitted to pedigree selection methods. The maximum benefits of recurrent selection programs can only be realized by the ap-

Table 8-24. Agronomic data for four single crosses evaluated at four locations for 10 yr (1976-1985) in Iowa.†

Cross	Yield Mg ha ⁻¹	Grain moisture	Lodging		Dropped ears
			Root	Stalk	
			%		
B14A × Mo17	7.28	20.6	11.4	7.6	1.0
B37 × Mo17	7.74	22.6	16.4	16.6	1.2
B73 × Mo17	8.51	22.4	15.2	9.8	1.7
B84 × Mo17	9.56	22.9	12.1	10.8	0.8
LSD (0.05)	0.38	0.5	4.8	3.8	--

† 37 location-yr environments; three tests discarded. Yield: B84 > B73 > B37 > B14A = 12.3, 10.0, and 6.3%, respectively.

plication of pedigree selection methods to isolate superior genotypes. Recurrent selection, therefore, was designed to enhance the probabilities of obtaining superior genotypes by pedigree selection. Recurrent selection was not designed to replace pedigree selection, but to supplement.

An example that illustrates the complementary benefits of recurrent selection and pedigree selection is provided by BS13 (Russell, 1986). BS13 was under half-sib family selection, and the S₁ progenies of the superior half-sib families used in recombination were also included in the breeding nursery for further selection, inbreeding, and testing. Four selections were eventually identified and released for use as possible parental stocks to produce hybrids. Lines, which have proved to be useful in hybrids, include B14 and B37 from the C0, B73 from the C5, and B84 from the C7 cycles of BS13. Each of the lines was crossed to a common inbred tester (Mo17) and evaluated at four Iowa locations for 10 yr (Table 8-24). In crosses with Mo17, B73 contributed a yield gain of 11.4% compared with B37, and B84 had a yield gain of 11.3% over B73. Total yield gain from the first C0 release (B14) to the C7 release (B84) was 31.3%, which is 4.5% cycle⁻¹ for the lines derived from selection within BS13. It is in this context that recurrent selection can be an integral part of applied breeding programs.

8-3 HETEROSIS AND HETEROTIC PATTERNS

The pure-line hybrid concept suggested by Shull (1909) has been used to exploit heterosis in corn breeding. Heterosis in crosses between cultivars and between inbred lines has been measured and is usually expected. Although heterosis is expressed in crosses, the specific genetic basis of heterosis in corn has not been resolved. Because of the divergent views presented to explain the phenomenon of heterosis, extensive research relative to breeding methods, inbred-line development, choice of testers, and selection methods for germplasm improvement has been conducted to determine the genetic basis of heterosis. The two primary views for the genetic basis of heterosis are generally classified as being due to primarily overdominant effects at individual loci vs. loci showing partial to complete dominance. Definitive evidence supporting the op-

posing views has not been obtained. Studies to determine the primary importance of different types of genetic effects have been conducted in genetic materials that ranged from genetically broad-based populations to crosses between inbred lines. Relative importance of the different types of genetic effects have varied relative to the types of materials studied, which is to be expected. Estimates of genetic effects with genetically broad-based populations suggest additive effects are of greater importance than either dominance (e.g., Gardner et al., 1953; Robinson et al., 1958; Gardner and Lonnquist, 1959) or epistatic effects (e.g., Silva and Hallauer, 1975). Comparisons of different types of crosses (single, three-way, and double) among inbred lines and different generations (parents, F_1 , F_2 , F_3 , and backcrosses) suggest nonadditive effects may be of some importance (Martin and Hallauer, 1976; Schnell and Singh, 1978; Moreno-Gonzalez and Dudley, 1981; Melchinger et al., 1986). The divergent results can be interpreted to support one of the opposing views for the cause of heterosis. Generally, it seems that the preponderance of evidence supports the view that heterosis in corn results from the accumulation of loci with alleles having partial to complete dominance. Some of the theories suggested for the expression of heterosis and evidence and interpretation supporting the different theories have been presented by East (1936), Jones (1945, 1952), Crow (1948), Brieger (1950), and Sprague (1953).

The formulation of the conditions necessary for heterosis of quantitatively inherited traits was given by Falconer (1981). He derived an expression for midparent (average of parents) heterosis (H) that considered the joint effects of all loci that differed in the cross of two particular lines or populations as $H = \Sigma dy^2$; d includes the effects due to dominance and, therefore, heterosis depends on the occurrence of dominance; and y^2 is the square of the difference in allele frequency between the lines or populations and determines the amount of heterosis expressed in the cross. Some level of dominance and differences in allele frequency, therefore, are necessary for the expression of heterosis. If either one is zero, no heterosis will be expressed, and the expression does not preclude partial, complete, or overdominant effects being the predominant types of effects. Falconer (1981) also emphasized that directional dominance is necessary, but the absence of heterosis does not preclude dominance at individual loci because of cancellation effects among loci. Heterosis is also specific for each cross, because different crosses will have different Σdy^2 values.

The differences in allele frequency and the directional dominance of the loci of the inbred lines and cultivars included in crosses are generally unknown. Hence, empirical data obtained from experiments that included the crosses and their respective parents were the only methods available to determine the level of heterosis expressed in the crosses. The estimates of heterosis in the crosses were expressed either on the basis of the midparents or the higher parents. The newer methods of analyses at the molecular level may refine the techniques for estimating heterosis

of crosses in the future. Development of genetic markers either with allozymes (Kahler et al., 1986) or with restriction fragment length polymorphisms for unique DNA sequences (Helentjaris et al., 1986) provides genetic information for inbred lines and cultivars. Based on the differences for the genetic markers, the expression of heterosis may become more predictable.

Beal (1877, p. 41–59) reported the first yield data from controlled crosses of corn cultivars. After Beal's experiments, crosses among cultivars were frequently produced and compared with the parental cultivars. Richey (1922) summarized data for 244 crosses and reported 86.5% were above midparent, 13.5% were below midparent, and 67.8% exceeded the higher parent. The empirical data established that some crosses were better than the higher parent, but their predictability was not based on any observed trends. Richey (1922) stated, "In such more or less haphazard crossing, therefore, the chances seem about equal of obtaining a cross that is or is not better than the better parent." Because of the emphasis given to exploiting heterosis of crosses among inbred lines, interest in variety crosses decreased after the first two decades of the 20th century. Interest in cultivar crosses was revived when consideration was given to the selection of populations to include in recurrent selection programs and to determine the level of relationship among cultivars. Information of this nature, for example, was reported by Robinson et al. (1956) for open-pollinated cultivars adapted to southeastern USA and by Lonnquist and Gardner (1961) for open-pollinated cultivars adapted to the U.S. Corn Belt. Moll et al. (1962) and Moll et al. (1965) extended the range of inferred diversity, based on geographical origin, among the open-pollinated cultivars included for producing variety crosses. Moll et al. (1962) reported that the relative heterosis expressed in the variety crosses agreed with the original classification of the presumed genetic divergence of the parental cultivars. But the concept of genetic diversity also seemed to have limits relative to the maximum expression of heterosis. Moll et al. (1965) found that the heterosis expressed in crosses between cultivars hypothesized to be most genetically diverse was less than heterosis between cultivars considered to be less genetically diverse.

Hallauer and Miranda (1981) included summaries of the heterosis expressed between cultivar crosses, including the data summarized by Richey (1922). The expression of heterosis, on the average, was similar for the studies conducted before 1932 and after 1955. The comparisons included 611 cultivars and 1394 cultivar crosses. For the cultivar crosses tested before 1932, 80.9% exceeded the midparent, whereas 90.0% of the cultivar crosses tested after 1955 exceeded the midparent. There was no general consensus among the studies in choice of cultivars included in the crosses and how the information on heterosis of the crosses was related to the overall classification of cultivars for establishing heterotic patterns. Some evidence suggested greater heterosis was expressed more consistently by crossing cultivars having different endosperm types (Ri-

chey, 1922), but other studies that included cultivars with different endosperm types (dent, flint, and floury) showed that the expressed heterosis was as great between cultivars having similar endosperm types as between those having different endosperm types (Paterniani and Lonnquist, 1963). Estimates of heterosis and combining ability are available in the literature, but the estimates are restricted to the specific sets of parent cultivars included. If a specific variety was included with a different set of cultivars, different estimates would be obtained. Because of the manner in which the parental cultivars were chosen and the absence of common checks to compare estimates among the different trials, information is not available to suggest the primary heterotic patterns among cultivars adapted to a given area.

The preferred approach would be to cross all of the landrace cultivars in a diallel series of crosses to permit direct comparisons. This approach, however, is no more feasible than crossing all of the available inbred lines in a diallel series of crosses to determine the best single crosses. The testcross method of evaluations was developed to permit preliminary screening of inbred lines to estimate their relative combining abilities. It seems a similar approach will be needed to determine the heterotic patterns among cultivars. But the same problem exists as in the choice of testers to evaluate inbred lines; i.e., what are the best testers? Can we assume that Reid Yellow Dent and Lancaster Sure Crop are the best testers to compare U.S. Corn Belt cultivars?

An example that illustrates the problem of identifying heterotic patterns among corn cultivars was addressed by Tsotsis (1972) and Kauffmann et al. (1982). They acknowledged there was a vast number of germ-plasm collections available that had not been evaluated and used by U.S. corn breeders. They selected nine open-pollinated cultivars and evaluated the 36 crosses among the cultivars for yield, and calculated the midparent heterosis for each cross (Table 8-25). Because the Reid Yellow Dent by Lancaster Sure Crop heterotic pattern has received greatest use in the U.S. Corn Belt programs, they were interested in determining if other possible heterotic patterns were available. Midparent heterosis for Reid Yellow Dent by Lancaster Sure Crop was 15%, which was similar to Lancaster Sure Crop by Hays Golden (15%), Reid Yellow Dent by Osterland Yellow (14%), and Reid Yellow Dent by Hays Golden (14%). The Leaming by Midland cross showed 21% midparent heterosis while Midland by Lancaster Sure Crop (33%) and Leaming by Lancaster Sure Crop (34%) also exhibited heterosis greater than the Reid Yellow Dent by Lancaster Sure Crop. Based on the data in Table 8-25, the heterotic pattern of Midland by Leaming was chosen to develop breeding populations for future development of lines that could be used to exploit the heterosis expressed in hybrids of their crosses. One breeding population included those cultivars which in crosses to Leaming were similar to Midland, and the second breeding population included those cultivars which in crosses with Midland were similar to Leaming. In an attempt

Table 8-25. Yields (Mg ha⁻¹) of nine U.S. open-pollinated cultivars (diagonal) and their diallel crosses (above diagonal) and estimates of midparent heterosis (%; below diagonal) of the cultivar crosses. Adapted from Kauffmann et al. (1982).

Cultivar	Cultivar									$\bar{x}$ (Mg ha ⁻¹)
	Midland	Lancaster Sure Crop	Reid Yellow Dent	Leaming	Krug	Late Clarage	Osterland Yellow	Golden Glow	Hay's Golden	
Midland	6.04	6.99	6.22	6.43	6.21	6.06	6.72	5.98	6.09	6.34
Lancaster Sure Crop	133†	4.49	5.79	6.05	5.71	6.17	5.62	5.67	5.41	5.93
Reid Yellow Dent	107	115	5.53	4.85	4.63	4.84	5.86	5.11	5.93	5.41
Leaming	121	134	96	4.54	5.88	5.77	6.28	5.77	6.40	5.93
Krug	112	120	88	123	5.02	5.61	6.49	5.21	6.64	5.80
Late Clarage	104	123	87	115	106	5.53	5.92	5.88	6.11	5.79
Osterland Yellow	124	121	114	134	132	115	4.80	5.72	5.71	6.04
Golden Glow	111	123	100	125	107	115	120	4.72	6.14	5.69
Hays Golden	111	115	114	136	134	117	118	128	4.89	6.05
$\bar{x}$	115.4	123.0	102.6	123.0	115.2	110.2	122.2	116.1	121.6	5.89

† Estimates of midparent heterosis calculated as $F_1[(P_1 + P_2)/t^{-1} \times 100$.

to classify other U.S. Corn Belt accessions, crosses of 111 cultivar accessions to Midland and Leaming were evaluated; Midland and Leaming were selected as the testers based on information from the diallel. Based on the crosses with Midland and Leaming, 27 accessions were assigned to the Midland population and 48 were assigned to the Leaming population. Recurrent selection was initiated within the two populations to develop useful germplasm sources for future line development that would be expected to have above average heterosis in crosses between the two populations. This approach seems logical for identifying a heterotic pattern, and then including additional germ plasm in the populations that reacted similarly to the selected heterotic pattern.

Heterotic patterns are of great concern to corn breeders, but it does not seem they were established in a systematic manner. They were established empirically by relating the heterosis observed in crosses with the origin of the parents included in the crosses. Heterotic patterns per se were not developed in an evolutionary sense, but heterotic patterns do occur because of selection, both artificial and natural, that has occurred in the development of the open-pollinated cultivars. The heterotic pattern identified by Tsotsis (1972) and Kauffmann et al. (1982) included two open-pollinated cultivars that originated in different regions of the U.S. Corn Belt. Leaming was developed in southern Ohio, and Midland was developed in southeastern Kansas. Allele frequencies affecting grain production in Leaming and Midland were undoubtedly different for many loci because of the different forces of selection in the two distinct regions. The presumed allele frequency differences for grain production were reflected in the phenotypic differences of the two open-pollinated cultivars: Midland has a later, taller, wider leaf plant type having a shorter ear with greater number of kernel rows than Leaming which was earlier, has less robust plant type, and has a more slender ear. Midland also has greater drought tolerance and greater resistance to first-generation European corn borer.

Tsotsis (1972) and Kauffmann et al. (1982) reported 15% midparent heterosis for Lancaster Sure Crop by Reid Yellow Dent, which was 50% less than for Midland by Lancaster Sure Crop (33%), Leaming by Lancaster Sure Crop (34%), Leaming by Osterland Yellow (34%), or Leaming by Hayes Golden, (34%) (Table 8-25). Average midparent heterosis for all crosses that included either Leaming or Lancaster Sure Crop as one parent was 23%. Except for Leaming and Lancaster Sure Crop, a common trend for the level of heterosis expressed in the crosses included a cultivar from the eastern areas of the U.S. Corn Belt crossed with one from the western areas. These trends seem reasonable and consistent because there would be less exchange of materials and chances of intermating of cultivars developed in the more remote areas. Hence, the chances for greater differences in allele frequencies seem reasonable.

Kauffmann et al. (1982) selected the Leaming by Midland heterotic pattern because of considerations other than the level of heterosis. The

example illustrates, however, how the concept of heterotic patterns was established. They were derived by breeders based on experience, breeding, and testing. Kauffmann et al. (1982), for example, could have established other heterotic patterns. After heterotic patterns have been established, further breeding efforts are planned to enhance and optimize the selected heterotic pattern. The selected heterotic patterns have a strong impact on the breeding materials chosen for selection. It may be difficult for mature breeding programs to make significant changes in heterotic patterns if they are heavily involved with line recycling. If changes are made in heterotic groups, a significant portion of the recovered lines may not be directly applicable.

Heterotic patterns are arbitrary. Although the Lancaster Sure Crop by Reid Yellow Dent heterotic pattern has received greatest attention in the U.S. Corn Belt, other heterotic patterns that included Leaming and Midland are considered. The number of heterotic patterns considered by a research organization depends on the extent of the breeding programs. They tend to be open-ended populations with other materials being added on the basis of their tested affinities. The choice of heterotic pattern used depends on the frequency of high-performance hybrids obtained for the lines derived from the respective source populations. Lines obtained from respective heterotic patterns tend to complement one another to maximize hybrid performance. The single-cross hybrid, B73 $\times$ Mo17, illustrates how inbred-line components contribute to the single cross (Fig. 8-9). B73 was derived from Iowa Stiff Stalk Synthetic (an improved synthetic population representative of Reid Yellow Dent) and Mo17 was derived by pedigree selection from the cross of (187-2 $\times$ C103). C103 was derived from Lancaster Sure Crop whereas 187-2 was derived from Krug, an improved strain of Reid Yellow Dent. B73 having greater number of kernel rows with greater number of kernels per ear and Mo17 having greater ear length and kernel size produce a consistently high performance single cross. The example for B73 $\times$ Mo17 also illustrates that the distinction between heterotic patterns is not absolute. Mo17 was derived from a cross that included one line with Reid Yellow Dent germ plasm (187-2) and one line with Lancaster Sure Crop germ plasm (C103). Mo17 is phenotypically more similar to C103 than 187-2 and is more similar to C103 in crosses with lines having Reid Yellow Dent germ plasm. Although not as good as B73 $\times$ Mo17, B37 $\times$ B73 also is a good performance single cross, and both lines were derived from Iowa Stiff Stalk Synthetic. B37 was derived from the first sampling, whereas B73 after five cycles of half-sib family selection (Table 8-24). It seems that the effects of sampling and selection were sufficient to cause different frequencies of alleles, resulting in heterosis in the cross of B37 $\times$ B73. Heterotic patterns do not preclude identifying superior crosses within populations, but the chances are greater between populations of identified heterotic patterns.

Concerns for heterotic patterns are not limited to U.S. Corn Belt.

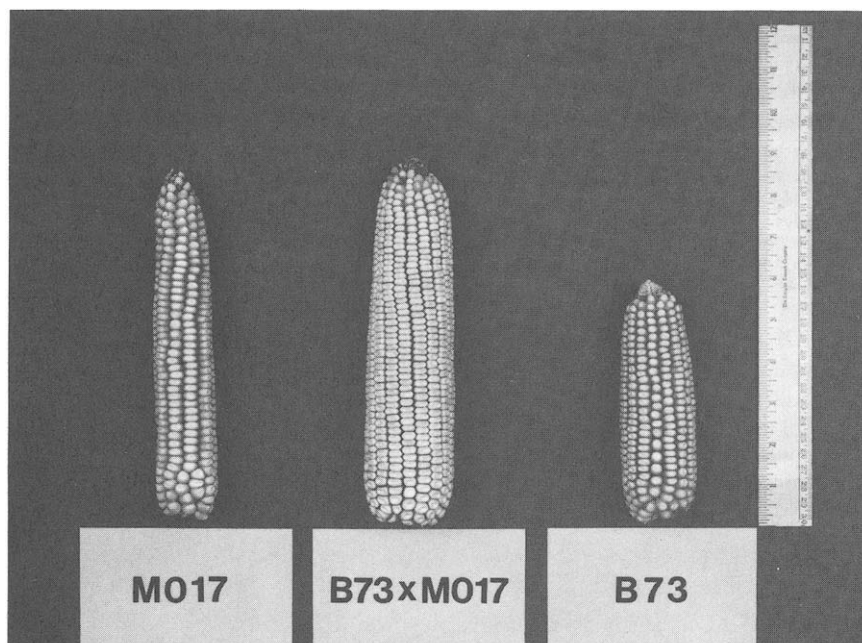


Fig. 8-9. An illustration of the heterotic pattern commonly used in the U.S. Corn Belt. B73 $\times$ Mo17 includes one line (B73) representative of Reid Yellow Dent and one line (Mo17) representative of Lancaster Sure Crop.

Heterotic patterns are considered in other important corn production areas of the world, where they seem to have arisen in the same manner as those for the U.S. Corn Belt. In Europe, a common heterotic pattern includes U.S. dent lines crossed with European flint lines; good seedling vigor for cool conditions with earlier maturity of the European flints complement the high productivity of U.S. dent lines. But the French single-cross, F2 $\times$ F6, included two lines derived from the same open-pollinated cultivar, and the single cross was widely used in Europe. In Mexico, crosses that include lines from ETO Composite and Tuxpeño are an important heterotic pattern, but the wealth of germ plasm available in Mexico would not preclude other important heterotic patterns. Flint-by-dent crosses are widely used in Brazil and usually include lines derived from either Cateto by Tuxpeño or Suwan I by Tuxpeño. Because of the requirement for endosperm type in Argentina, a common heterotic pattern includes crosses of flint lines with recovered flint lines, which have a dent background to enhance productivity. The heterotic pattern of ETO Composite by Tuxpeño has been widely considered in tropical regions of the world, but the heterotic pattern that includes Suwan I and Tuxpeño seems to be receiving greater attention.

Based on testcross evaluations of tropical races, Goodman (1985) listed 10 heterotic patterns that have been identified and exploited by breeders in the tropical areas: Cuban Flint by Tuxpeño, Cuban Flint by

Tuson, Tuson by Tuxpeño, Coastal Tropical Flint (Caribbean Flint) by Chandelle, Cuban Flint by Coastal Tropical Flint, Tuxpeño by Coastal Tropical Flint, Tuson by Chandelle, Tuxpeño by ETO, Chandelle by Haitian Yellow, and Cuban Flint by Perla. For the 10 heterotic patterns, only eight races are included because Cuban Flint and Tuxpeño were included in four crosses and Tuson, Coastal Tropical Flint, and Chandelle in three crosses. The crosses among the tropical races illustrated the same pattern shown by Kauffmann et al. (1982) for crosses among domestic open-pollinated cultivars; i.e., some races or cultivars expressed greater heterosis in crosses than others. One interesting heterotic pattern was Tuson by Tuxpeño because both races expressed heterosis in crosses with Cuban Flint. To reduce the number of heterotic patterns for breeding purposes in the tropical areas, it seems emphasis should be given to the races Tuxpeño, Cuban Flint, Tuson, Coastal Tropical Flint, and Chandelle. Two of the races (Tuxpeño and Caribbean Flint) also were selected by Gerrish (1983) for adaptation and use in temperate areas. For breeders in the temperate areas to exploit the heterosis among the tropical areas, the tropical materials will need to be adapted to temperate areas to provide valid comparisons with adapted materials. Oyervides-Garcia et al. (1985) and Gutierrez-Gaitan et al. (1986) compared crosses between and within cultivars from Mexico and the U.S. Corn Belt and tested in Mexico and the western U.S. Corn Belt; no useful information was obtained for crosses between Mexican cultivars and between Mexican and U.S. Corn Belt cultivars in the U.S. Corn Belt because the adverse photoperiod response masked the expression for other traits. Goodman (1985), however, identified Tuson by U.S. Southern Dents as a potentially useful heterotic pattern for use in southern U.S. corn breeding programs.

Heterotic patterns are a fact-of-life and important to corn breeders. Greater emphasis is given to the consideration of heterotic patterns by some than by others. Some heterotic patterns have been used in the past and will continue to be considered, whereas others will be identified and developed. Some heterotic patterns are transported to other areas of the world where the materials are adaptable. If heterotic patterns are important in some areas, but the materials are unadapted, efforts will be made to adapt and exploit them in crosses with native materials (Gerrish, 1983).

8-4 GENOTYPE $\times$ ENVIRONMENT INTERACTION

Genotype $\times$ environment (GE) interaction is the differential performance of genotypes across environments. The existence of GE interaction necessitates that breeders evaluate genotypes in more than one environment to obtain repeatable rankings of genotypes. The detection of GE interaction by means of an analysis of variance, however, does not indicate how the genotypes are interacting. If there are g genotypes and e environments then there are $(ge)!$ possible types of interactions

(Allard and Bradshaw, 1964). The large number of interactions possible demonstrates the need for types of analysis that would summarize for the breeder how genotypes interact with one another across environments.

The class of methods, called *stability analysis*, has provided the tools by which breeders can summarize the overall performance of cultivars across environments. The definition of a stable cultivar varies with the type of stability analysis used, but generally breeders want cultivars with high mean yield that respond to improved environments. The predominant type of stability analysis used has been regression of cultivar means on environmental means. This type of analysis has been referred to as joint regression analysis (Freeman, 1973).

Joint regression analysis of GE interaction involves the regression of cultivar means on some index of the environment. The analysis provides an estimate of the linear response of individual genotypes to environments (b_1) and an estimate of the deviations of the observed values from the predicted values (deviations mean square). The computational methodology has been presented and will not be reviewed (Eberhart and Russell, 1966; Perkins and Jinks, 1968; Wright, 1971; Freeman and Perkins, 1971; Shulka, 1972; Hardwick and Wood, 1972; Hill, 1976; Lin et al., 1986; Westcott, 1986). Although joint regression analysis has been frequently used in many species, statistical problems have limited its application and interpretation. The primary problems with the analysis are defining the environmental index and assuming a linear relationship between GE interaction effects and the environmental index.

The environmental index is the measure of the environment used to assess its inherent productivity. For lack of a better measure, most joint regression analyses have used the mean of the cultivars grown in an environment as the index [environmental mean] (Yates and Cochran, 1938; Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Perkins and Jinks, 1968; Tai, 1971). Unbiased estimates of the regression coefficients are obtained only if the environmental index is measured without error (Freeman and Perkins, 1971; Hardwick and Wood, 1972; Hill, 1976). When the environmental mean is used as the index of the environment, the regression coefficient is biased and often underestimated (Hardwick and Wood, 1972; Wright, 1976). The bias depends on the ratio of the environmental variation to the error mean square and the number of cultivars. When the ratio and/or the number of cultivars are large the bias will be small, but not necessarily negligible. Reducing the bias to zero seems to be impossible, because all measures of environmental productivity will have an associated error. Therefore, the environments and numbers of cultivars should be selected to minimize the bias.

Freeman and Perkins (1971) criticized the use of environmental means as the index because the environmental means are not independent of the cultivar means. Freeman (1973) later qualified this criticism stating that when working with two-way tables one may consider the marginal

means fixed when making inferences about values in the table. This is equivalent to working with a model containing only fixed effects (Hill, 1976). However, this does not eliminate problems associated with the distribution of degrees of freedom (df) in the analysis of variance table (Freeman and Perkins, 1971). In the Eberhart-Russell (1966) analysis, the environment and GE sums of squares (SS) are pooled (to obtain the environment within genotype SS) and the resulting $g(e-1)$ (where there are g varieties and e environments) df are partitioned into three parts: the environment-linear SS with one df; the variety $\times$ environment-linear SS with $g-1$ df; and pooled deviations with $g(e-1)$ df. The pooled deviations SS are then partitioned into g components (one for each variety) with $e-2$ df. This approach has been criticized because the environment-linear SS are equal to the environment SS, but they are assigned one and $e-1$ df, respectively (Freeman and Perkins, 1971; Freeman, 1973). The assignment of df in the Eberhart-Russell analysis should be $e-1$ for the environment-linear SS; $g-1$ for the cultivar $\times$ environment-linear SS and $(g-1)(e-2)$ for the pooled deviations SS. This assignment of df does not allow the deviation MS for each cultivar to be tested for significance against the error MS. The deviation MS for individual cultivars, however, can be compared using Bartlett's test for comparing g variances each with $e-2$ df (Freeman and Perkins, 1971). Freeman and Perkins (1971) presented the appropriate analysis when using an independent index of the environment.

Several alternative measures of environmental effects are available other than the environment mean (Freeman and Perkins, 1971). One suggestion is to divide the replications into two groups and use one replication as a measure of environmental effects and use the others to measure the interaction. At least three replications would be needed to obtain an estimate of experimental error. Another suggestion is to include checks solely for the purpose of estimating environmental effects. Presumably, one would want the checks to be elite cultivars that are widely grown in the region. Many checks, however, may be needed to provide an accurate assessment of the environments. Freeman and Perkins (1971) have suggested that the coefficient obtained from regression of the mean of all cultivars on the environmental index can be tested to see if it differs significantly from one, and the residual from this regression can be tested against the experimental error. If neither of these tests is significant, the environmental index can be regarded as an estimate of the true environmental effects.

Mather and Caligari (1974) suggested that each cultivar be regressed on the mean of the other cultivars. This method avoids the criticisms made by Freeman and Perkins (1971) when regressions are done on the environmental mean. Also, additional cultivars do not need to be grown to assess environmental effects. The computational aspects of the method proposed by Mather and Caligari are increased and may be time consuming without the aid of computer software capable of matrix algebra.

Moll et al. (1978), using the modification suggested by Mather and Caligari (1974), showed that the regression coefficients are a function of responsiveness of cultivars to environments and the correlation of the responses of cultivars in different environments.

Pederson et al. (1978) suggested the gene pool concept as a measure of the environmental index. They defined the gene pool as "... a sample of genes representative of currently acceptable or commercially grown germ plasm for a specific geographic area." The concept was suggested to allow comparisons between cultivars grown in different locations and years. One problem associated with this approach is that environmental means will tend to increase with time, as older cultivars are replaced with improved cultivars, even though the environments may not have improved. The procedure also seems to be plagued with statistical problems, because cultivar means and stability parameters are estimated from different environments.

Perhaps the most desirable environmental index would be one composed of climatic, edaphic, and management variables (Hardwick and Wood, 1972; Westcott, 1986). Westcott (1986) states that the linear regression of cultivars on environmental means cannot be regarded as trustworthy and cannot be recommended for analysis of GE interactions. He supports further investigations into the effects of environmental variables on crop yields. Knight (1970) reached a similar conclusion, but recognized that the joint regression analysis "... is a valuable technique for the plant breeder when making a broad study of a collection of varieties." To use environmental variables in the study of GE interactions, variables are needed that explain a significant portion of the variation among environments. Little work has been reported along these lines because it is difficult, time-consuming, and expensive to measure these types of variables. Hardwick and Wood (1972) have shown how regression on environmental variables relates to regression on environment means.

The joint regression analysis requires the assumption that the relationship between the GE interaction and the environmental index is linear. This assumption has been the subject of criticism and is considered a valid reason for not using the analysis (Westcott, 1986). The linear relationship between cultivar and mean performance will hold when variation in cultivar performance between environments can be described by a linear function of environmental variables (climatic, edaphic, and management) and when the residuals from this regression are not significantly larger than experimental error (Hardwick and Wood, 1972). Westcott (1986) criticized the linear regression approach because outliers can influence the estimates of stability parameters for a cultivar. Westcott (1986) cited examples which supported his position, but failed to cite the many examples where the linear regression approach has performed well. To illustrate the effect of one or two environments on estimates of stability parameters, Westcott used an example with only six environments. While it is difficult to determine the number of environments needed to

accurately estimate stability, clearly more than six are needed. In many applied breeding programs, cultivars may be grown in 20 to 100 environments and one or two deviant environments will have little effect on the estimates of stability parameters from the joint regression analysis.

Breeders often have data available from cultivar trials in which the cultivars vary among locations and years. These trials often contain checks which may be the same across locations within a year, but may vary with years as higher yielding checks become available. The analysis of these types of data using conventional joint regression analyses is difficult if not impossible because the experiment is unbalanced (not all genotype-environment cells contain an observation). Zhang and Geng (1986) have proposed a technique using joint regression analysis to handle this situation. Their method involves dividing the environments into three periods. Period I includes the trials in which older check cultivars are used. Period II is a transition period where older check cultivars are grown with newer check cultivars. Period III is the environments in which only the newer check cultivars are grown. The method involves regressing the check means on the environmental means in Period II. The cultivars under test are then regressed on the older check cultivars in Period I and all other cultivars are regressed on the newer check cultivars. Comparisons among cultivars are made possible by reparameterizing the stability parameters using the regression of the check cultivars on the environment means. Zhang and Geng (1986) demonstrated the use of their method for cotton (*Gossypium hirsutum* L.) cultivar trials.

Other methods for analysis of GE interaction are available. These include cluster analysis, principal components analysis, geometrical methods, and stochastic dominance. Westcott (1986) has reviewed the use of these methods and provides an inclusive reference list. He concludes his review by stating that the linear (joint) regression analysis is unsatisfactory and that the defects of this method cannot be overcome by cluster analysis or principal component analysis. Westcott (1986) recommends further research into environmental variables, stochastic dominance, multidimensional scaling, and correspondence analysis. Westcott, however, failed to recognize the plant breeding aspects of joint regression analysis and the fact that the analysis has been successful in identifying cultivars breeders wish to select.

Prior to the development of stability analyses, comparisons of cultivar stability were based primarily on GE mean squares and components of variance. These measures indicate little about how the cultivars are interacting and simply measure the magnitude of the interaction. The GE interaction SS can analytically be partitioned into differences in cultivar responsiveness and changes in rank order across environments (Cockerham, 1963; Moll et al. 1978). Corn breeders are primarily interested in discarding cultivars that show large rank order changes across environments; however, as Comstock (1977) has suggested, plant breeders and quantitative geneticists have devoted little effort to how rank order changes relate to genetic and GE variance.

Comstock and Moll (1963) emphasized the importance of defining both the cultivars and environmental reference populations when studying GE interactions. Robinson (1959) illustrated this point by comparing the results of Sprague and Federer (1951) from trials conducted in Iowa with results of yield trials conducted in North Carolina. The results of Sprague and Federer's study indicated that cultivar-year interactions were of primary importance, whereas Robinson found the second-order interaction cultivar-year-location was more important than the first-order interactions. Although the results of the two studies are not directly comparable because they involve different types of genetic material, they do indicate that results of GE interaction studies cannot be extrapolated to regions outside of the target populations of environments.

Scott (1967) demonstrated that it was possible to select for stability when defined as a cultivar that exhibits the least yield variation over all environments in the test. The response of cultivars to environments is primarily a property of the line or additive genetic effects; however, the stability of cultivars (the deviation from regression in the Eberhart-Russell model) seems to be associated with all types of gene action (Eberhart and Russell, 1966, 1969). The ability of corn to respond to environments by producing two ears seems to be a primary mechanism contributing to the stability of corn hybrids (Collins et al., 1965; Russell and Eberhart, 1968; Russell and Prior, 1975; Cross, 1977).

Eberhart and Russell (1966) analyzed several sets of corn yield trials and reported that cultivars with high mean yield generally have regression coefficients greater than one. This relationship suggests that by selecting for high mean yield, breeders are also selecting for cultivars that respond to favorable environments (Rosielle and Hamblin, 1981). Gama and Hallauer (1980) compared hybrids that were selected and unselected for grain yield and found no differences in the frequency of stable hybrids in the two groups. A significant correlation was reported between mean yield and the regression coefficient, although it was too small to be of predictive value. They suggested that hybrids should first be screened for mean yield over environments and then selection should be made among the elite hybrids for stability over environments.

The selection of the type of stability analysis to use in ranking cultivars depends on both definition of stability used and the objectives of the breeding program. Some breeders desire cultivars which perform consistently across environments (i.e., yield the same in all environments) while others desire cultivars that respond to improved environments. The first type of stability has been referred to as the "biological concept of stability" and the second type has been referred to as the "agronomic concept of stability" (Becker, 1981). Becker (1981) correlated four measures of stability using data from five different crops. The four measures of stability were variation among environments within cultivars, coefficient of regression, the deviations mean square from the Eberhart-Russell analysis, and Wricke's (1962) ecovalence. The correlations between the

within variance and regression coefficient, and between ecovalence and the regression mean square were large ($r \geq 0.81^{**}$) and consistent across crops. Becker (1981) made three points concerning these relationships: (i) the regression coefficient is equivalent to the within variance as a measure of stability according to the biological concept; (ii) the deviation mean square is equivalent to ecovalence as a measure of the agronomic concept of stability; and (iii) the use of different concepts of stability will lead to different rankings of genotypes, because the two parameters are uncorrelated with each other. Becker (1981) concluded that the two parameters from the Eberhart-Russell analysis, when used together, provide the most comprehensive analysis of stability according to the defined concepts.

Nor and Cady (1979) studied the feasibility of using physical measures of the environment as the environmental index. They had measurements on rainfall, mean daily temperature, and growing degree days for each of 36 environments. The environmental index was the first principal component from the pooled sample variance-covariance matrix of the environmental variables. The model used was the same as that suggested by Freeman and Perkins (1971) for independent environmental indices. They compared this technique with the Eberhart-Russell analysis. The rank correlation between coefficient of regressions for the two techniques was 0.69 with 16 df. There were some notable rank changes, but in general the two techniques ranked variety responses similarly. They did not compare deviation mean squares for the two techniques. The favorable results from this study indicate the need for more extensive studies on the use of environmental variables as indices of environments.

There are two differing views on the types of environments to use in developing and testing corn breeding materials (Lambert, 1984). One view contends that corn breeding materials should be developed and evaluated in environments typical of the target population of environments. The premise of this view is that some environmental factors will often be limiting and breeding materials should be developed under these conditions. The other view contends that breeding materials should be developed under nonlimiting environmental conditions and the breeding material should not be under stress for any environmental factors. The premise of this view is that nonlimiting environmental conditions will allow the expression of all genes, providing for greater genotypic variation and ultimately larger genetic gains.

Rosielle and Hamblin (1981) considered the theoretical aspects of selection for yield in stress and nonstress environments. They considered selection for tolerance to stress conditions and selection for high mean productivity. If yield in nonstress environments is defined as Y_1 and yield in stress environments is defined Y_2 , then selection for tolerance is equivalent to selecting for high $Y_2 - Y_1$ and selection for mean productivity is equivalent to selecting for high $(Y_1 + Y_2)/2$. They found that selection for tolerance will normally result in a reduction in mean yield in nonstress

environments (Y_i) and to obtain a yield increase in nonstress environments genetic variation in stress environments must be greater than in nonstress environments. Selection for mean productivity, however, will usually result in a yield increase in both stress and nonstress environments. This would only result in a yield decrease in nonstress environments when genetic variance in stress environments is greater than in nonstress environments, and when there is a negative genetic correlation between yield in stress and nonstress environments. Rosielle and Hamblin (1981) concluded that the most desirable approach would be to choose testing sites to be representative of population of environments for which the breeder wishes to improve mean yield.

Lambert (1978, 1984) initiated a reciprocal recurrent selection program in which testing was done under high-yield environmental conditions and under normal environmental conditions. He reported that genetic variance for grain yield was greater under high-yield environmental conditions than under normal environmental conditions, except in 1 yr when the high-yield environment was stressed by hail damage. The genetic correlations between the high-yield environment and normal environment were positive and 8 of the 12 correlations reported were significantly different from zero. These results seem to support the conclusion of Rosielle and Hamblin (1981) that selection should be conducted in environments representative of the target population of environments.

Determining the location of test sites is perhaps the most difficult challenge facing corn breeders. Generally, when a breeder is moving into a new locality little information is available on GE interaction. Corn breeders are often assigned the task of breeding for a particular maturity zone, which reduces the target population of environments considerably, although decisions on the locations of test sites still must be made so that efficient use of available resources are made and differences among cultivars are maximized. Without prior knowledge of the nature of the GE interaction in a given target population of environments, breeders must locate test sites based on prior knowledge of the germ plasm, climatic, edaphic, and management factors, and the overall objectives of the breeding program. Once information on GE interaction becomes available it can be used to add and delete locations so that available resources are used most efficiently.

The optimum allocation of test sites depends on whether breeders are developing cultivars for a specific set of environmental conditions or whether the cultivars will be grown over a wide range of environments. With corn there is a tendency for cultivars to spread geographically throughout the maturity zone to which they are adapted. The consequences of this are that corn breeders must develop cultivars that perform consistently throughout the range of environments likely to be encountered in a maturity zone.

Several criteria have been proposed for selecting test sites. Allen et al. (1978) concluded that if environments vary substantially in their value

as test sites it is because of variation among them in the correlation between cultivar value in test environments and cultivar value in the target population of environments. Hamblin et al. (1980) suggested that criteria for choosing test sites should be: (i) that yields of selected cultivars at the test site consistently correspond to their yield over the range of environments for which they are intended; (ii) that the test site maximize yield differences among cultivars; and (iii) that the test site be consistently high yielding. Brown et al. (1983) presented a method to choose optimum test sites by first clustering test sites based on environmental variables and then identifying the optimum test sites within clusters by linear regression on a cultivar index. Correlations between environments and the concept of a reference set of cultivars have been suggested as a method to select test sites representative of a target population of environments (Fox and Rosielle, 1982a).

Multivariate techniques have been used extensively for grouping environments and cultivars to improve the efficiency of breeding programs. The primary technique used has been cluster analysis. The performance of the cluster technique depends on the type of data analyzed, the clustering algorithm, and the cluster method (Fox and Rosielle, 1982b; Lin, 1982; Ramey and Rosielle, 1983).

8-5 INDEX SELECTION

Corn breeders are seldom interested in improving one trait at a time. When the correlation between two traits is large and negative, selection for one trait will produce an undesirable correlated response. Klenke et al. (1986) found that four cycles of selection for European corn borer resistance resulted in a corresponding decrease in grain yield; consequently, they concluded that grain yield should be included in the selection criteria when selecting for corn borer resistance. Martin and Russell (1984) reported that three cycles of selection for stalk strength and stalk-rot resistance resulted in significantly reduced grain yields. These are just two of the many examples of undesirable correlated responses that can result from single trait selection.

Index selection is a procedure that combines all the information available on an individual or family to aid in the selection of those with the highest aggregate breeding value. When making selections, breeders often have a mental image of the type of plant or family they wish to select. They combine this image with the data obtained on the family and use the combined information to make their selections. Essentially, breeders are constructing a mental selection index. The mental selection index may work well when a small number of families is evaluated; however, with large numbers of families the procedure lacks repeatability and response to selection is difficult to predict. A formal selection index, when properly constructed, has both repeatability and predictability, which allows statements to be made about future performance before selections

are made. The objective of a selection index is to find a linear combination of phenotypic values that maximizes the expected gain in aggregate breeding value.

Smith (1936) developed the first index for selecting plant lines using Fisher's (1936) discriminant function. Hazel (1943) developed the same index using the method of path coefficients and outlined methods for estimating genetic variances and covariances. This index is known as the *Smith-Hazel index*. The Smith-Hazel index is a linear index of the form $I = \sum_{i=1}^n b_i P_i$, where n is the number of traits in the index, P_i is the observed phenotypic value of the i th trait, and b_i is the weighting factor assigned to the i th trait. The b_i 's are calculated to maximize the expected gain in the economic value of an individual or family (aggregate genotype). The aggregate genotype of an individual or family is defined as $H = \sum_{i=1}^m a_i G_i$, where m is the number of traits used in defining the aggregate genotype, G_i is the genotypic (breeding) value of the i th trait, and a_i is the relative economic value of the i th trait. Maximizing the expected genetic gain in the aggregate genotype is equivalent to: (i) maximizing the correlation of the sample index (I) with true breeding value (H); (ii) minimizing the expected value of the squared deviations between I and H ; and (iii) maximizing the probability of correct selection (Williams, 1962). Henderson (1963), Lin (1978), and Baker (1986) reviewed the theory of the construction of selection indices.

Several modifications of the Smith-Hazel index have been developed. One modification is the restricted selection index (Kempthorne and Nordskog, 1959; James, 1968; Cunningham et al., 1970; Lin, 1985). The objective of the restricted selection index is to maximize genetic gain in some traits while holding genetic gain in other traits to zero or some fixed constant (Tallis, 1962). Smith et al. (1981a) suggested that the traits in the index be weighted by the product of their economic value and heritability. These weights are the solutions to the Smith-Hazel index equations when the genotypic and phenotypic correlations are assumed to be zero. The simplified index is nearly as efficient as the Smith-Hazel index when the absolute value of the genetic and phenotypic correlations are <0.30 . Lin (1978) reported that estimated error of the genetic correlation has a larger effect on efficiency of index selection than estimated error of heritability.

Sampling errors in the estimation of genotypic and phenotypic variances and covariances can have large effects on the accuracy of the selection index and can cause biases in predicted gains (Lin, 1978). Brim et al. (1959) suggested that each trait be weighted by the relative economic value when sampling errors of parameter estimates are large. This index is called the *base index* (Williams, 1962). The Smith-Hazel index is expected to be more efficient than the base index unless sampling errors of parameter estimates are large (Williams, 1962; Lin, 1978). The primary advantages of the base index are simplicity of use, freedom from error or parameter estimation, and the index can be used in situations where estimates of genetic parameters are not available.

Economic values of the various traits breeders wish to select are rarely known and few studies have been conducted to determine how economic values should be assigned to traits. Because of these difficulties, a class of selection indices that are weight-free have been developed. Elston's (1963) weight-free index (EWF) ranks individuals on the basis of the product of their phenotypic values. Equal value is assigned to the traits by subtracting the minimum acceptable phenotype from all traits before the index is calculated. An additional advantage of EWF is that estimates of genotypic and phenotypic parameters are not needed in its construction. Because EWF is curvilinear, theory is not available to predict gains for this index. However, Baker (1974) found that EWF can be approximated by a linear index (BSD) with weights equal to the reciprocals of the phenotypic standard deviations. Approximate predicted gains can then be calculated using the theory developed by Smith (1936).

The rank summation index (RSI) suggested by Mulamba and Mock (1978) is also weight free. Rank summation index is calculated by ranking the cultivars for the traits of interest and then summing the ranks over traits. If the cultivars are ranked with one being good and there are three traits in the index, then an index value of three would represent the best variety in the sample. The primary advantages of RSI are that genotypic and phenotypic parameter estimates are not needed, the data are transformed so that the phenotypic variances for each trait are identical, and economic values are not needed, although they can be used when known (Crosbie et al., 1980). Crosbie et al. (1980) reported that predicted gains for BSD are good approximations of predicted gains for RSI. Rank summation index is most efficient when heritabilities are high and of similar magnitude among traits, and when the correlations among traits are favorable or approximately zero (Smith et al. 1981b).

The desired gain index (DGI) suggested by Pesek and Baker (1969) does not require specification of economic values, but it does require estimates of genetic variances and covariances. The DGI is calculated by substituting gains the breeder desires for each trait in the predicted gain equation for the Smith-Hazel index and solving the resulting equations for the index weights. Desired gain index is developed under the assumption that desired gains are easier to specify than economic values.

Selection index theory can also be used to make selections based on information from relatives (Henderson, 1963). Information from relatives is used to increase the accuracy of selection defined as the correlation of the sample index with the aggregate genotype. Moreno-Gonzalez and Hallauer (1982) outlined a procedure to combine information on S_2 families per se with information on full-sib families from a reciprocal recurrent selection program. The resulting selection index is superior to reciprocal full-sib selection when the heritability of the trait under selection is low and the advantage is increased when the correlations between the S_2 and full-sib families are large relative to the heritabilities.

Index selection is at least as efficient as independent culling levels

and independent culling levels is at least as efficient as tandem selection (Hazel and Lush, 1942; Lin, 1978). The relative efficiency of index selection methods depends on progeny type, number of traits in the index, relative economic values assigned to the traits, selection intensity, and the relative magnitude of the genotypic and phenotypic variances and covariances among traits included in the index. As a general rule, expected genetic gain for one trait from selecting on an index containing (n) traits is only $1/\sqrt{n}$ times as great as selection for that trait alone (Hazel and Lush, 1942).

Long-term recurrent selection experiments using selection indices as the criteria of selection are rare. Generally, studies designed to compare methods of index selection in plants involve only one or two cycles of selection with a different index being used in each cycle of selection. The most common method of comparing selection indices is to use predicted gains and selection differentials. Predicted gains and selection differentials for a given trait from index selection are usually represented as a percentage of the value obtained for single trait selection. Cunningham (1969) presented a method for comparing the relative efficiencies of selection indices.

Subandi et al. (1973) compared two variations of EWF, two Smith-Hazel indices differing only in the economic values assigned to the traits, a base index, and selection for each trait alone using predicted gains. The traits were grain yield, percentage of lodged plants, and percentage of dropped ears. They concluded that EWF would be the most useful because correlations between traits were low, the index does not require specification of economic values, and is parameter free. Compton and Lonnquist (1982) reported on four cycles of intrapopulation full-sib recurrent selection using the index suggested by Subandi et al. (1973). Observed gains for yield averaged 4.7% cycle⁻¹, but no significant changes were reported for percentage of upright plants and plants without dropped ears, although trends were in the desired direction. They concluded that selection based on their index may result in yield gains similar to other studies where selection is for yield per se. West et al. (1980) studied the performance of EWF with replicated S_1 and reciprocal full-sib recurrent selection and concluded that EWF has proved its ability to change traits involved in the index simultaneously in the desired direction.

Widstrom (1974) constructed three selection indices to aid in selection for resistance to ear damage caused by corn earworm [*Heliothis zea* (Boddie)]. The traits included in the indices were corn earworm injury, husk tightness, days to 50% pollen shed, and husk extension. The first index (RS) was the Smith-Hazel index constructed using genotypic and phenotypic covariance matrices obtained from evaluating S_1 lines. The second index (RI) was constructed in the same manner except that standardized direct and correlated responses were substituted for the genotypic covariance matrix. The third index (RSI) was constructed by substituting

the standardized direct and correlated responses when selection was for corn earworm injury for the index weights. The indices derived from realized gains are expected to be as efficient as the Smith-Hazel index when expected and observed responses to selection are comparable. Experimental evidence supported this conclusion.

Widstrom et al. (1982) evaluated response to four cycles of S_1 recurrent selection using the three selection indices derived by Widstrom (1974). The selection indices were not modified during the course of the recurrent selection experiment. An additional selection experiment was conducted for corn earworm injury. Significant improvement for corn earworm injury was obtained only for the RSI and RI selection indices. Selection for RI and corn earworm injury tended to increase husk tightness whereas selection for RS and RSI resulted in looser husks. The RSI and RS increased husk extension and RI and corn earworm injury decreased husk extension. All four selection methods resulted in populations that were 1 to 2 d earlier in reaching anthesis. Correlations between traits included in the index were changed over cycles of selection by all selection criteria. These changes were attributed to a breakup of genetic linkages and suggested that new indices should be constructed to exert the desired selection pressure for the traits of interest in future cycles of selection. The authors concluded that RI produced the best results.

Suwantaradon et al. (1975) compared the Smith-Hazel index, base index, and the desired gain index for S_1 recurrent selection to improve seven agronomic traits of corn. Two sets of arbitrary economic values were used with the Smith-Hazel index and in both instances the performance of the index was less than satisfactory because undesirable responses were obtained for four of the seven traits included in the indices. The base index was 95 to 97% as efficient as the Smith-Hazel index and should be used instead of the Smith-Hazel index when the relative economic weights are known, heritabilities are high, and the correlations among the traits are low. When the desired gain index was used the final goals of the program would be obtained after 14 cycles of recurrent selection. The desired gain index is preferred when relative economic values are difficult to specify.

The performance of selection indices is dependent on obtaining accurate estimates of the phenotypic and genotypic variances and covariances. Moll et al. (1975) evaluated the performance of five selection indices and concluded that nonlinear relationships between traits will have considerable effect on the prediction of correlated selection responses. The responses of traits included in the index were more variable than responses to index selection. Kauffmann and Dudley (1979) evaluated seven selection indices designed to improve corn grain yield, percentage of protein, and kernel weight simultaneously. They reported good agreement between observed and predicted responses to index selection and concluded that genetic variance and covariance estimates obtained from

200 half-sib families were sufficiently accurate to be useful in the development of selection indices. Miles et al. (1981) reached a similar conclusion, but found that selection on indices to simultaneously improve resistance to four corn diseases was no more effective than selection for disease score per se.

Crosbie et al. (1980) compared predicted gains for three cold tolerance traits of corn using several selection indices. Predicted gains for DGI were sensitive to the relative amount of economic gain specified for each trait. The Smith-Hazel and base indices ranked lines similarly. There were problems, however, with these indices because the variances for each trait differed substantially, and these indices were designed to maximize gain in the aggregate genotype. The authors suggested that RSI, EWF, or BSD be used to improve composite traits, like cold tolerance, which are composed of individual traits without logical economic values. These indices have the advantage of being parameter free, simple to use, and do not require the specification of economic values.

St. Martin et al. (1982) evaluated the use of restricted selection indices for the improvement of *opaque-2* corn. The indices were constructed to simultaneously improve agronomic and protein and kernel quality characteristics of *opaque-2* corn. They evaluated four classes of indices that differed in the traits included in the indices. The most efficient indices were those with four or five traits. When more than five traits were included the indices were less effective and singular variance-covariance matrices became more frequent. They found that the most effective trait combinations in the indices were not dependent on the recurrent selection scheme under consideration. The most efficient indices relied on direct rather than indirect selection response and these indices were generally free of the problems associated with parameter estimation. They concluded that the successful application of selection indices requires a measure of subjective judgement on the part of the breeder.

Most of the empirical work in corn involving the comparisons of selection indices have generally favored the use of indices that are parameter free and do not require specification of relative economic values. The successful application of selection indices to corn improvement will depend on the goals of the breeding program, the genetic material under selection, and the definition of the aggregate genotype. Selection indices are sensitive to inaccurate estimates of genotypic and phenotypic parameters and changes in relative economic values of the traits. More research is needed on methods of assigning economic values to traits in selection indices. Accurate estimates of variances and covariances are essential if selection indices are to be useful to corn breeders. It is particularly important to have accurate estimates of the covariances, which evidently are the most difficult to estimate. The empirical evidence reviewed suggests that it is not possible to make general statements about the best selection index.

REFERENCES

- Acosta, A.E., and P.L. Crane. 1972. Further selection for lower ear height in maize. *Crop Sci.* 12:165-167.
- Allard, R.W., and A.D. Bradshaw. 1964. Implications of genotype-environment interactions in applied plant breeding. *Crop Sci.* 4:503-508.
- Allen, F.L., R.E. Comstock, and D.C. Rasmusson. 1978. Optimal environments for yield testing. *Crop Sci.* 18:747-751.
- Altman, D.W., and R.H. Busch. 1984. Random intermating before selection in spring wheat. *Crop Sci.* 24:1085-1089.
- Anonymous. 1972. Corn. Genetic vulnerability of major crops. NAS-NRC, Washington, DC.
- Bailey, T.B., Jr. 1977. Selection limits in self-fertilizing populations following the cross of homozygous lines. p. 399-412. *In* E. Pollak et al. (ed.) *Proc. Int. Conf. Quant. Genet.*, Iowa State Univ., Ames. 16-21 Aug. 1976. Iowa State Univ. Press, Ames.
- , and R.E. Comstock. 1976. Linkage and the synthesis of better genotypes in self-fertilizing species. *Crop Sci.* 16:363-370.
- Baker, R.J. 1974. Selection indices without economic weights for animal breeding. *Can. J. Anim. Sci.* 54:1-8.
- . 1986. Selection indices in plant breeding. CRC Press, Boca Raton, FL.
- Balko, L.G., and W.A. Russell. 1980a. Effects of rates of nitrogen fertilizer on maize inbred lines and hybrid progeny. I. Prediction of yield response. *Maydica* 25:65-79.
- , and ———. 1980b. Effects of rate of nitrogen fertilizer on maize inbred lines and hybrid progeny. II. Correlations among agronomic traits. *Maydica* 25:81-94.
- Bauman, L.F. 1959. Evidence of non-allelic gene interaction in determining yield, ear height, and kernel row number in corn. *Agron. J.* 51:531-534.
- . 1977. Improvement of established maize inbreds. *Maydica* 22:213-222.
- . 1981. Review of methods used by breeders to develop superior corn inbreds. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 36:199-208.
- Beal, W.J. 1877. Report of the professor of botany and horticulture. Michigan Board of Agric., Lansing.
- Becker, H.C. 1981. Correlations among some statistical measures of phenotypic stability. *Euphytica* 30:835-840.
- Bogenschütz, T.G., and W.A. Russell. 1986. An evaluation for genetic variation within inbred lines maintained by sib-mating and self-pollination. *Euphytica* 35:403-412.
- Bos, I. 1977. More arguments against intermating F_2 plants of a self-fertilizing crop. *Euphytica* 26:33-46.
- Brieger, F.G., 1950. The genetic basis of heterosis in maize. *Genetics* 35:420-445.
- Brim, C.A. 1966. A modified pedigree method of selection in soybeans. *Crop Sci.* 6:220.
- , H.W. Johnson, and C.C. Cockerham. 1959. Multiple selection criteria in soybeans. *Agron. J.* 51:42-46.
- Brown, K.D., M.E. Sorrells, and W.R. Coffman. 1983. A method for classification and evaluation of testing environments. *Crop Sci.* 23:889-893.
- Brown, W.L. 1975. A broader germplasm base in corn and sorghum. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 30:81-89.
- Burton, G.W. 1982. Developing superior inbreds from exotic germplasm of pearl millet. *Crop Sci.* 22:653-655.
- Busch, R.H., and W.A. Russell. 1964. Hybrid expression of mutations affecting quantitative characters in inbred lines of *Zea mays* L. *Crop Sci.* 4:400-402.
- Carlone, M.R., and W.A. Russell. 1987. Response to three plant densities and four nitrogen levels for four maize cultivars from each of seven ears of breeding. *Crop Sci.* 27:465-470.
- Castleberry, R.M., C.W. Crum, and C.F. Krull. 1984. Genetic yield improvement of U.S. maize cultivars under varying fertility and climatic environments. *Crop Sci.* 24:33-36.
- Centro Internacional Mejoramiento de Maiz y Trigo. 1982. CIMMYT Review 1982. CIMMYT, El Batán, Mexico.
- . 1984. CIMMYT research highlights 1984. CIMMYT, El Batán, Mexico.
- Chase, S.S. 1952. Production of homozygous diploids of maize from monoplasts. *Agron. J.* 44:263-267.

- Collier, J.W. 1959. Three cycles of reciprocal recurrent selection. *Proc. Annu. Hybrid Corn. Ind. Res. Conf.* 14:12-23.
- Collins, W.K., W.A. Russell, and S.A. Eberhart. 1965. Performance of two-ear type of corn belt maize. *Crop Sci.* 5:113-116.
- Compton, W.A., and R.E. Comstock. 1976. More on modified ear-to-row selection. *Crop Sci.* 16:122.
- , and J.H. Lonnquist. 1982. A multiplicative selection index applied to four cycles of full-sib recurrent selection in maize. *Crop Sci.* 22:981-983.
- , R.F. Mumm, and B. Mathema. 1979. Progress from adaptive mass selection in incompletely adapted maize populations. *Crop Sci.* 19:531-533.
- Comstock, R.E. 1964. Selection procedures in corn improvement. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 19:87-94.
- . 1977. Quantitative genetics and the design of breeding programs. p. 705-718. *In* E. Pollak et al. (ed.) *Proc. Int. Conf. Quant. Genet.*, Iowa State Univ., Ames. 16-21 Aug. 1976. Iowa State Univ. Press, Ames.
- . 1979. Inbred lines vs. the populations as testers in reciprocal recurrent selection. *Crop Sci.* 19:881-886.
- , and R.H. Moll. 1963. Genotype-environment interactions. p. 164-196. *In* W.D. Hanson and H.F. Robinson (ed.) *Statistical genetics and plant breeding*. Pub. 982. NAS-NRC, Washington, DC.
- , H.F. Robinson, and P.H. Harvey. 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. *Agron. J.* 41:360-367.
- Covarrubias-Prieto, Jorge. 1987. Genetic variability in F_2 maize populations before and after random mating. Ph.D. diss. Iowa State Univ., Ames (Diss. Abstr. 48:923-B).
- Crosbie, T.M. 1092. Changes in physiological traits associated with long-term breeding efforts to improve grain yield of maize. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 37:206-223.
- , J.J. Mock, and O.S. Smith. 1980. Comparison of gains predicted by several selection methods for cold tolerance traits of two maize populations. *Crop Sci.* 20:649-655.
- Cross, H.Z. 1977. Interrelationships among yield stability and yield components in early maize. *Crop Sci.* 6:357-360.
- Crow, J.F. 1948. Alternative hypothesis of hybrid vigor. *Genetics* 33:477-487.
- Cunningham, E.P. 1969. The relative efficiencies of selection indexes. *Acta Agric. Scand.* 19:45-48.
- , R.A. Moen, and T. Gjedrem. 1970. Restriction of selection indexes. *Biometrics* 26:67-74.
- Darrah, L.L. 1986. Evaluation of population improvement in the Kenya maize breeding methods study. p. 160-175. *In* To feed ourselves. *Proc. 1 Eastern, Central, and Southern Africa Regional Maize Workshop*, Lusaka, Zambia. 10-17 Mar. 1985. CIMMYT, El Batan, Mexico.
- , S.A. Eberhart, and L.H. Penny. 1978. Six years of maize selection in 'Kitale Synthetic II', 'Ecuador 573', and 'Kitale Composite A' using methods of the comprehensive breeding systems. *Euphytica* 27:191-204.
- Davis, R.L. 1927. Report of the plant breeder, p. 14-15. *In* Puerto Rico Agric. Exp. Stn. Annu. Rep.
- Devey, M.E., and W.A. Russell. 1983. Evaluation of recurrent selection for stalk quality in a maize cultivar and effects of other agronomic traits. *Iowa State J. Res.* 58:207-219.
- Dodd, J.L. 1980. A photosynthetic stress-translocation balance concept of corn stalk rot. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 32:122-130.
- Doupnik, B., Jr., Les Lane, and David Wysong. 1981. Nebraska corn variety tests for reaction to corn lethal necrosis. 1981 Results. Nebraska Coop. Ext. Serv. Rep. UNL-SCS-81-151.
- Dudley, J.W. 1977. Seventy-six generations of selection for oil and protein percentage in maize. p. 459-473. *In* E. Pollak et al. (ed.) *Proc. Int. Conf. Quant. Genet.*, Iowa State Univ., Ames. 16-21 Aug. 1976. Iowa State Univ. Press, Ames.
- . 1982. Theory of transfer of alleles. *Crop Sci.* 22:631-637.
- . 1984a. A method of identifying lines for use in improving parents of a single cross. *Crop Sci.* 24:355-357.
- . 1984b. Identifying parents for use in a pedigree breeding program. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 39:176-188.

- . 1984c. A method for identifying populations containing favorable alleles not present in elite germplasm. *Crop Sci.* 24:1053–1054.
- . 1988. Evaluation of maize populations as sources of favorable alleles. *Crop Sci.* 28:486–491.
- , and R.J. Lambert. 1969. Genetic variability after 65 generations of selection in Illinois high oil, low oil, high protein, and low protein strains of *Zea mays* L. *Crop Sci.* 9:179–181.
- , and R.H. Moll. 1969. Interpretation and use of estimates of heritability and genetic variances in plant breeding. *Crop Sci.* 9:257–262.
- Duvick, D.N. 1974. Continuous backcrossing to transfer prolificacy to a single-eared inbred line of maize. *Crop Sci.* 14:69–71.
- . 1977. Genetic rates of gain in hybrid maize yields during the past 40 years. *Maydica.* 22:187–196.
- . 1984. Genetic contributions to yield gains of U.S. hybrid maize, 1930 to 1980. p. 15–47. *In* W.R. Fehr (ed.) Genetic contributions to yield gains of five major crop plants. Spec. Pub. 7. CSSA, Madison, WI.
- Earle, E.D., and V.E. Gracen. 1985. Somaclonal variation in progeny of plants from corn tissue culture. p. 139–152. *In* R.R. Henke et al. (ed.) Tissue culture in forestry and agriculture. Plenum Press, New York.
- East, E.M. 1908. Inbreeding in corn. 1907. p. 419–428. *In* Connecticut Agric. Exp. Stn. Rep.
- . 1936. Heterosis. *Genetics* 21:375–397.
- Eberhart, S.A. 1970. Factors affecting efficiencies of breeding methods. *Afr. Soils* 15:669–680.
- , S. Debela, and A.R. Hallauer. 1973. Recurrent selection in the BSSS and BSCB1 maize varieties and half-sib selection in BSSS. *Crop Sci.* 13:451–456.
- , M.N. Harrison, and F. Ogada. 1967. A comprehensive breeding system. *Zuchter* 37:169–174.
- , and W.A. Russell. 1966. Stability parameters in comparing varieties. *Crop Sci.* 6:36–40.
- , and ———. 1969. Yield and stability for a 10-line diallel of single-cross and double-cross maize hybrids. *Crop Sci.* 9:357–361.
- Edallo, C., C. Zucchini, M. Perenzin, and F. Salamini. 1981. Chromosome variation and frequency of spontaneous mutants associated with in vitro culture and plant regeneration in maize. *Maydica* 26:39–56.
- El-Hifny, M.A., M.S. Ahmund, J.D. Smith, and A.J. Bockholdt. 1969. Gamete selection with an inbred tester. *Theor. Appl. Genet.* 39:379–381.
- El-Lakany, M.A., and W.A. Russell. 1971. Relationship of maize characters with yield in testcrosses of inbreds at different plant densities. *Crop Sci.* 11:698–701.
- Elston, R.C. 1963. A weight free index for the purpose of ranking or selection with respect to several traits at a time. *Biometrics* 19:85–97.
- Falconer, D.S. 1981. Introduction to quantitative genetics. Longman, New York.
- Finlay, K.W., and G.W. Wilkinson. 1963. The analysis of adaptation in a plant breeding programme. *Aust. J. Agric. Res.* 14:742–754.
- Fleming, A.A. 1971. Performance of stocks within long-time inbred lines of maize in testcrosses. *Crop Sci.* 11:620–622.
- , and G.M. Kozelnicky. 1965. Sibbing versus selfing in the maintenance of inbred lines of corn and the attainment of homozygosity. *Crop Sci.* 5:303–304.
- , ———, and E.B. Browne. 1964. Variations between stocks within long-time inbred lines of maize (*Zea mays* L.). *Crop Sci.* 4:291–295.
- Fox, P.N., and A.A. Rosielle. 1982a. Reference sets of genotypes and selection for yield in unpredictable environments. *Crop Sci.* 22:1171–1175.
- , and ———. 1982b. Reducing the influence of environmental main-effects on pattern analysis of plant breeding environments. *Euphytica* 31:645–656.
- Freeman, G.H. 1973. Statistical methods for the analysis of genotype-environment interactions. *Heredity* 31:339–354.
- , and J.M. Perkins. 1971. Environmental and genotype-environmental components of variability. VIII. Relation between genotypes grown in different environments and measures of these environments. *Heredity* 27:15–23.
- Frey, K.J. 1971. Improving crop yields through plant breedings. p. 15–58. J.D. Eastin and R.D. Munson (ed.) Moving off the yield plateau. Spec. Pub. 20. ASA, CSSA, and SSSA, Madison, WI.
- Gama, E.E.G.e., and A.R. Hallauer. 1977. Relation between inbred and hybrid traits in maize. *Crop Sci.* 17:703–706.

- , and ----. 1980. Stability of hybrids produced from selected and unselected lines of maize. *Crop Sci.* 20:623-626.
- Gardner, C.O. 1961. An evaluation of effects of mass selection and seed irradiation with thermal neutrons on yield of corn. *Crop Sci.* 1:241-245.
- . 1977. Quantitative genetic studies and population improvement in maize and sorghum. p. 475-489. *In* E. Pollak et al. (ed.) *Proc. Int. Conf. Quant. Genet.* Iowa State Univ., Ames, 16-21 Aug. 1976. Iowa State Univ. Press, Ames.
- . 1978. Population improvement in maize. p. 207-228. *In* D.B. Walden (ed.) *Maize breeding and genetics.* John Wiley and Sons, New York.
- , P.H. Harvey, R.E. Comstock, and H.F. Robinson. 1953. Dominance of genes controlling quantitative characters in maize. *Agron. J.* 45:186-191.
- , and J.H. Lonnquist. 1959. Linkage and the degree of dominance of genes controlling quantitative characters in maize. *Agron. J.* 51:524-528.
- Gerrish, E.E. 1983. Indication from a diallel study for interracial maize hybridization in the Corn Belt. *Crop Sci.* 1082-1084.
- Gevers, H.O. 1975. Three cycles of reciprocal recurrent selection in maize under two systems of plant selection. *Agroplante* 7:107-108.
- Giesbrecht, J. 1964. Gamete selection in two early maturing corn varieties. *Crop Sci.* 4:653-655.
- Goodman, M.M. 1985. Exotic maize germplasm: Status, prospects, and remedies. *Iowa State J. Res.* 59:497-527.
- Goodsell, S. 1961. Male sterility in corn by androgenesis. *Crop Sci.* 1:227-228.
- Gorsline, G.W. 1961. Phenotypic epistasis for ten quantitative characters in maize. *Crop Sci.* 1:55-58.
- Grogan, C.O., and C.A. Francis. 1972. Heterosis in inbred source crosses of maize (*Zea mays* L.). *Crop Sci.* 12:729-730.
- Gutierrez-Gaitan, M.A., H. Cortez-Mendoza, E.N. Wathika, C.O. Gardner, M. Oyervides-Garcia, A.R. Hallauer, and L.L. Darrah. 1986. Testcross evaluation of Mexican maize populations. *Crop Sci.* 26:99-104.
- Hallauer, A.R. 1967. Development of single-cross hybrids from two-eared maize populations. *Crop Sci.* 7:192-195.
- . 1970. Zygote selection for the development of single-cross hybrids in maize. *Adv. Front. Plant Sci.* 25:75-81.
- . 1972. Third phase in yield evaluation of synthetic varieties of maize. *Crop Sci.* 12:16-18.
- . 1973. Hybrid development and population improvement in reciprocal full-sib selection. *Egypt. J. Genet. Cytol.* 1:84-101.
- . 1975. Relation of gene action and type of testers in maize breeding procedures. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 30:150-165.
- . 1979. Corn breeding opportunities in the 1980's. Iowa Seed Dealers' Assoc., Des Moines.
- . 1981. Selection and breeding methods. p. 3-55. *In* K.J. Frey (ed.) *Plant breeding II.* Iowa State Univ. Press, Ames.
- . 1984. Reciprocal full-sib selection in maize. *Crop Sci.* 24:755-759.
- . 1985. Compendium of recurrent selection methods and their application. *Crit. Rev. Plant Sci.* 3:1-34.
- , and S.A. Eberhart. 1966. Evaluation of synthetic varieties of maize for yield. *Crop Sci.* 6:423-427.
- , and ----. 1970. Reciprocal full-sib selection. *Crop Sci.* 10:315-316.
- , and E. Lopez-Perez. 1979. Comparisons among testers for evaluating lines of corn. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 34:57-72.
- , and D. Malithano. 1976. Evaluation of maize varieties for their potential as breeding populations. *Euphytica* 25:117-127.
- , and J.B. Miranda, Fo. 1981. Quantitative genetics in maize breeding. Iowa State Univ. Press, Ames.
- , and J.H. Sears. 1968. Second phase in the evaluation of synthetic varieties of maize for yield. *Crop Sci.* 8:448-451.
- , and ----. 1969. Mass selection for yield in two varieties of maize. *Crop Sci.* 9:47-50.
- , W.A. Russell, and O.S. Smith. 1983. Quantitative analysis of Iowa Stiff Stalk Synthetic. *Stadler Genet. Symp.* 15:83-104.

- Hamblin, J.H., M. Fisher, and H.I. Ridings. 1980. The choice of locality for plant breeding when selecting for high yield and general adaptation. *Euphytica* 29:161-168.
- Hardwick, R.C., and J.T. Wood. 1972. Regression methods for studying genotype-environment interactions. *Heredity* 28:209-222.
- Hayes, H.K., and R.J. Garber. 1919. Synthetic production of high protein corn in relation to breeding. *J. Am. Soc. Agron.* 11:308-318.
- , and I.J. Johnson. 1939. The breeding of improved selfed lines of corn. *J. Am. Soc. Agron.* 31:701-724.
- Hazel, L.N. 1943. The genetic basis for constructing selection indices. *Genetics* 28:476-490.
- , and J.L. Lush. 1942. The efficiency of three methods of selection. *J. Hered.* 33:393-399.
- Helentjaris, T., M. Slocum, S. Wright, A. Schaefer, and J. Nienhuis. 1986. Construction of genetic linkage maps in maize and tomato using restriction fragment length polymorphisms. *Theor. Appl. Genet.* 72:761-769.
- Helms, T.C. 1986. Evaluation of three recurrent selection methods in corn (*Zea mays* L.). Ph.D. diss. Iowa State Univ., Ames. (Diss. Abstr. 86-27115).
- Henderson, C.R. 1963. Selection index and expected genetic advances. p. 141-163. *In* W.D. Hanson and H.F. Robinson (ed.) *Statistical genetics and plant breeding*. Pub. 982. NAS-NRC, Washington, DC.
- Hill, J. 1976. Genotype-environment interactions—a challenge for plant breeders. *J. Agric. Sci.* 85:477-494.
- Hoard, K.G., and T.M. Crosbie. 1985. S₁ line recurrent selection for cold tolerance in two maize populations. *Crop Sci.* 25:1041-1045.
- Hoegemeyer, T.C., and A.R. Hallauer. 1976. Selection among and within full-sib families to develop single crosses of maize. *Crop Sci.* 16:76-81.
- Hooker, A.L. 1961. A new type of resistance to *Helminthosporium turcicum*. *Planta Dis. Rep.* 45:780-781.
- Hopkins, C.G. 1899. Improvement in the chemical composition of the corn kernel. *Bull.—Agric. Exp. Stn. (Ill.)* 55:205-240.
- Horner, E.S. 1985. Effects of selection for S₂ progeny versus testcross performance in corn. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 40:142-150.
- , H.W. Lundy, M.C. Lutrick, and W.H. Chapman. 1973. Comparison of three methods of recurrent selection in maize. *Crop Sci.* 13:485-489.
- , M.C. Lutrick, W.H. Chapman, and F.G. Martin. 1976. Effect of recurrent selection for combining ability with a single-cross tester in maize. *Crop Sci.* 16:5-8.
- Hull, F.H. 1945. Recurrent selection and specific combining ability in corn. *J. Am. Soc. Agron.* 37:134-145.
- , 1952. Recurrent selection and overdominance. p. 451-473. *In* J.W. Gowen (ed.) *Heterosis*. Iowa State Univ. Press, Ames.
- Humphrey, A.B., D.F. Matzinger, and C.C. Cockerham. 1969. Effects of random intercrossing in a naturally self-fertilizing species *Nicotiana tabacum* L. *Crop Sci.* 9:495-497.
- James, J.W. 1968. Index selection with restrictions. *Biometrics* 24:1015-1018.
- Jenkins, M.J. 1929. Correlation studies with inbred and cross-bred strains of maize. *J. Agric. Res.* 39:677-721.
- , 1935. The effect of inbreeding and of selection within inbred lines of maize upon hybrids made after successive generations of selfing. *Iowa State Coll. J. Sci.* 9:429-450.
- Jenkins, M.T. 1936. Corn improvement. p. 455-522. *In* Yearbook of agriculture, 1936. U.S. Gov. Print. Office, Washington, DC.
- , 1940. The segregation of genes affecting yield of grain in maize. *J. Am. Soc. Agron.* 32:55-63.
- , 1978. Maize breeding during the development and early years of hybrid maize. p. 13-28. *In* D.B. Walden (ed.) *Maize breeding and genetics*. John Wiley and Sons, New York.
- , and A.M. Brunson. 1932. Methods of testing inbred lines of maize in crossbred combinations. *J. Am. Soc. Agron.* 24:523-530.
- Jensen, S.D., W.E. Kuhn, and R.L. McConnell. 1983. Combining ability studies in elite U.S. maize germplasm. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 38:87-96.
- Jinahyon, S., and W.A. Russell. 1969. Evaluation of recurrent selection for stalk-rot resistance in an open-pollinated variety of maize. *Iowa State J. Sci.* 43:229-237.

- Johnson, E.C. 1963. Mass selection for yield in a tropical corn variety. p. 82. *In* Agronomy abstracts. ASA, Madison, WI.
- , K.S. Fisher, G.O. Edmeades, and A.F.E. Palmer. 1986. Recurrent selection for reduced plant height in lowland tropical maize. *Crop Sci.* 26:253-260.
- Johnson, G.R. 1980. Simple quantitative theory for selection during inbred line development. III. *Corn Breeders' School* 16:1-18.
- Jones, D.F. 1918. The effects of inbreeding and cross-breeding upon development. p. 5-100. *In* Connecticut Agric. Exp. Stn. Bull. 207.
- . 1945. Heterosis resulting from degenerative changes. *Genetics* 30:527-542.
- . 1952. Plasmagenes and chromogenes in heterosis. p. 224-235. *In* J.W. Gowen (ed.) *Heterosis*. Iowa State Univ. Press, Ames.
- Jones, L.P., W.A. Compton, and C.O. Gardner. 1971. Comparison of full and half-sib reciprocal recurrent selection. *Theor. Appl. Genet.* 41:36-39.
- Kahler, A.L., A.R. Hallauer, and C.O. Gardner. 1986. Allozyme polymorphisms within and among open-pollinated and adapted exotic populations of maize. *Theor. Appl. Genet.* 72:592-601.
- Kauffmann, K.D., and J.W. Dudley. 1979. Selection indices for corn grain yield, percent protein, and kernel weight. *Crop Sci.* 19:583-588.
- , C.W. Crum, and M.F. Lindsey. 1982. Exotic germplasm in a corn breeding program. III. *Corn Breeders' School* 18:6-39.
- Kemphorne, O., and A.W. Nordskog. 1959. Restricted selection indices. *Biometrics* 15:10-19.
- Kermicle, J.L. 1969. Androgenesis conditioned by a mutation in maize. *Science* 166:1422-1424.
- Klenke, J.R., W.A. Russell, and W.D. Guthrie. 1986. Recurrent selection for resistance to European corn borer in a corn synthetic and correlated effects on agronomic traits. *Crop Sci.* 26:864-868.
- Knight, R. 1970. The measurement and interpretation of genotype-environment interaction. *Euphytica* 19:225-235.
- Kuhn, H.C., and H.O. Gevers. 1980. Hybrid improvement in the past three decades. *Proc. South African Maize Breed. Symp.* 4:69-73.
- Lambert, R.J. 1978. Breeding corn in a non-limiting environment. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 33:24-33.
- . 1984. Reciprocal recurrent selection of maize in a high-yield environment. *Maydica* 29:419-430.
- Lamkey, K., and A.R. Hallauer. 1984. Comparisons of maize populations improved by recurrent selection. *Maydica* 29:357-374.
- , and ----. 1986. Performance of high $\times$ high, high $\times$ low, low $\times$ low crosses of lines from the BSSS maize synthetic. *Crop Sci.* 7:1114-1118.
- , and ----. 1987. Heritability estimated from recurrent selection experiments in maize. *Maydica* 32:61-78.
- Landi, P., E. Pe, and S. Conti. 1983. Effects of selection at medium and high competition levels on the performance of local maize. (*Zea mays* L.) lines. *Maydica* 38:45-51.
- Lantin, M.M. and A.R. Hallauer. 1981. Response to reciprocal full-sib and mass selection in corn (*Zea mays* L.). *Proc. Iowa Acad. Sci.* 88:172-178.
- Lee, M., J.L. Gadelmann, and R.L. Phillips. 1988. Agronomic evaluation of inbred lines derived from tissue cultures of maize. *Theor. Appl. Genet.* 75:841-849.
- Lerner, I. 1958. *The genetic basis of selection*. John Wiley and Sons, New York.
- Lin, C.S. 1982. Grouping genotypes by a cluster method directly related to genotype-environment interaction mean square. *Theor. Appl. Genet.* 62:277-280.
- , M.R. Binns, and L.P. Lefkovitch. 1986. Stability analysis: where do we stand? *Crop Sci.* 26:894-900.
- Lin, C.Y. 1978. Index selection for genetic improvement of quantitative characters. *Theor. Appl. Genet.* 52:49-56.
- . 1985. A simple stepwise procedure of deriving selection index with restrictions. *Theor. Appl. Genet.* 70:147-150.
- Lonnquist, J.H. 1949. The development and performance of synthetic varieties of maize. *Agron. J.* 41:153-156.
- . 1950. The effect of selection for combining ability within segregating lines of corn. *Agron. J.* 42:503-508.
- . 1964. A modification of the ear-to-row procedure for the improvement of maize populations. *Crop Sci.* 4:227-228.

- . 1967. Mass selection for prolificacy in maize. *Zuchter* 37:185–188.
- , and C.O. Gardner. 1961. Heterosis in intervarietal crosses in maize and its implications in breeding procedures. *Crop Sci.* 1:179–183.
- , and D.P. McGill. 1954. Gamete selection from selected zygotes in corn breeding. *Agron. J.* 46:147–150.
- , and N.E. Williams. 1967. Development of maize hybrids through selection among full-sib families. *Crop Sci.* 7:369–370.
- Mareck, J.H. and C.O. Gardner. 1979. Responses to mass selection in maize and stability of resulting populations. *Crop Sci.* 19:779–783.
- Marquez-Sanchez, F. 1982. Modifications to cyclic hybridization in maize with single-eared plants. *Crop Sci.* 22:314–319.
- Martin, J.M., and A.R. Hallauer. 1976. Relation between heterozygosis and yield for four types of maize inbred lines. *Egypt. J. Genet. Cytol.* 5:119–135.
- , and ———. 1980. Seven cycles of reciprocal recurrent selection in BSSS and BSCB1 maize populations. *Crop Sci.* 20:599–603.
- Martin, M.J., and W.A. Russell. 1984a. Response of a maize synthetic to recurrent selection for stalk quality. *Crop Sci.* 24:331–337.
- , and ———. 1984b. Correlated responses of yield and other agronomic traits to recurrent selection for stalk quality in a maize (*Zea mays* L.) synthetic. *Crop Sci.* 24:746–750.
- Mather, K., and P.D.S. Caligari. 1974. Genotype $\times$ environmental interactions. I. Regression of interaction on overall effect of the environment. *Heredity* 33:43–59.
- Matzinger, D.F. 1953. Comparison of three types of testers for the evaluation of inbred lines of corn. *Agron. J.* 45:493–495.
- McCoy, T.J., and R.L. Phillips. 1982. Chromosome stability in maize (*Zea mays* L.) tissue culture and sectoring in some regenerated plants. *Can. J. Genet. Cytol.* 24:559–565.
- Meghji, M.R. J.W. Dudley, R.L. Lambert, and G.F. Sprague. 1984. Inbreeding depression, inbred and hybrid grain yield, and other traits of maize representing three eras. *Crop Sci.* 24:545–549.
- Melchinger, A.E., H.H. Geiger, and F.W. Schnell. 1986. Epistasis in maize (*Zea mays* L.). I. Comparison of single and three-way cross hybrids among early flint and dent inbred lines. *Maydica* 31:179–192.
- Miles, J.W., J.W. Dudley, D.G. White, and R.J. Lambert. 1981. Response to selection for resistance to four diseases in two corn populations. *Crop Sci.* 21:980–983.
- Mock, J.J., and A.A. Bakri. 1976. Recurrent selection for cold tolerance in maize. *Crop Sci.* 16:230–233.
- , and R.B. Pearce. 1975. An ideotype of maize. *Euphytica* 24:613–623.
- Moll, R.H., C.C. Cockerham, C.W. Stuber, and W.P. Williams. 1978. Selection responses, genetic-environmental interactions, and heterosis with recurrent selection for yield in maize. *Crop Sci.* 18:641–645.
- , and W.D. Hanson. 1984. Comparisons of effects of intrapopulation vs. interpopulation selection in maize. *Crop Sci.* 24:1047–1052.
- , J.H. Lonnquist, J.V. Fortuna, and E.C. Johnson. 1965. The relation of heterosis and genetic divergence in maize. *Genetics* 52:139–144.
- , and H.F. Robinson. 1966. Observed and expected response in four selection experiments in maize. *Crop Sci.* 6:319–324.
- , W.S. Salhuana, and H.F. Robinson. 1962. Heterosis and genetic diversity in variety crosses of maize. *Crop Sci.* 2:197–198.
- , C.W. Stuber, and W.D. Hanson. 1975. Correlated responses and responses to index selection involving yield and ear height of maize. *Crop Sci.* 15:243–248.
- Moreno-Gonzalez, J., and J.W. Dudley. 1981. Epistasis in related and unrelated maize hybrids determined by three methods. *Crop Sci.* 21:644–651.
- , and A.R. Hallauer. 1982. Combined S_2 and crossbred family selection in full-sib reciprocal recurrent selection. *Theor. Appl. Genet.* 61:353–358.
- Mulamba, N.N., A.R. Hallauer, and O.S. Smith. 1983. Recurrent selection for grain yield in a maize population. *Crop Sci.* 23:536–540.
- , and J.J. Mock. 1978. Improvement of yield potential of the Eto Blanco maize (*Zea mays* L.) population by breeding for plant traits. *Egypt. J. Genet. Cytol.* 7:40–41.
- Murphy, R.P. 1942. Convergent improvement with four inbred liens of corn. *J. Am. Soc. Agron.* 34:138–150.
- Nor, K.M., and F.B. Cady. 1979. Methodology for identifying wide adaptability in crops. *Agron. J.* 71:556–559.

- Nordquist, P.T., O.J. Webster, C.O. Gardner, and W.M. Ross. 1973. Registration of three sorghum germplasm random mating populations. *Crop Sci.* 13:132.
- Oyervides-Garcia, M., and A.R. Hallauer. 1986. Selection-induced differences among strains of Iowa Stiff Stalk Synthetic maize. *Crop Sci.* 26:506-511.
- , ----, and H. Cortez-Mendoza. 1985. Evaluation of improved maize populations in Mexico and the U.S. Corn Belt. *Crop Sci.* 25:115-120.
- Paliwal, R.L., and E.W. Sprague. 1981. Improving adaptation and yield dependability in maize in the developing world. CIMMYT, El Batan, Mexico.
- Pandey, S., A.O. Diallo, T.M.T. Islam, and J. Deutsch. 1986. Progress from selection in eight tropical maize populations using international testing. *Crop Sci.* 26:879-884.
- Paterniani, E. 1978. Phenotypic recurrent selection for prolificacy in maize. *Maydica* 23:29-34.
- , and J.H. Lonnquist. 1963. Heterosis in interracial crosses of corn (*Zea mays* L.). *Crop Sci.* 504-507.
- , and R. Vencovsky. 1977. Reciprocal recurrent selection in maize (*Zea mays* L.) based on testcrosses of half-sib families. *Maydica* 22:141-152.
- Pederson, A.R., E.H. Everson, and J.E. Grafius. 1978. The gene pool concept as a basis for cultivar selection and recombination. *Crop Sci.* 18:883-886.
- Pederson, D.G. 1974. Arguments against intermating before selection in a self-fertilizing species. *Theor. Appl. Genet.* 45:157-162.
- Penny, L.H., G.E. Scott, and W.D. Guthrie. 1967. Recurrent selection for European corn borer resistance in maize. *Crop Sci.* 7:407-409.
- Perkins, J.M., and J.L. Jinks. 1968. Environmental and genotype-environmental components of variability. III. Multiple lines and crosses. *Heredity* 23:339-356.
- Pesek, J., and R.J. Baker. 1969. Desired improvement in relation to selection indices. *Can. J. Plant. Sci.* 49:803-804.
- Pinnell, E.L., E.H. Rinke, and H.K. Hayes. 1952. Gamete selection for specific combining ability. p. 378-388. *In* J.W. Gowen (ed.) *Heterosis*. Iowa State Univ. Press, Ames.
- Ramey, T.B., and A.A. Rosielle. 1983. HASS cluster analysis: A new method of grouping genotypes or environments in plant breeding. *Theor. Appl. Genet.* 66:131-133.
- Rawlings, J.C., and D.L. Thompson. 1962. Performance level as criterion for the choice of maize testers. *Crop Sci.* 2:217-220.
- Richey, F.D., 1922. The experimental basis for the present status of corn breeding. *J. Am. Soc. Agron.* 14:1-17.
- . 1927. The convergent improvement of selfed lines of corn. *Am. Nat.* 61:430-449.
- . 1947. Corn breeding, gamete selection, the Oenothera method and related miscellany. *J. Am. Soc. Agron.* 39:403-412.
- , and G.F. Sprague. 1931. Experiments on hybrid vigor and convergent improvement in corn. USDA Tech. Bull. 267. U.S. Gov. Print. Office, Washington, DC.
- Rinke, E.H., and J.C. Sentz. 1961. Moving corn-belt germ-plasm northward. *Proc. Annu. Hybrid Corn Ind. Conf.* 16:53-56.
- Robinson, H.F. 1959. The implications of environmental effects of genotypes in relation to breeding. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 14:24-31.
- , C.C. Cockerham, and R.H. Moll. 1958. Studies on the estimation of dominance variance and effects of linkage bias. p. 171-177. *In* O. Kempthorne (ed.) *Biometrical genetics*. Pergamon Press, New York.
- , R.E. Comstock, A. Klalil, and P.H. Harvey. 1956. Dominance versus overdominance in heterosis: Evidence from crosses between open-pollinated varieties of maize. *Am. Nat.* 90:127-131.
- Rosielle, A.A., and J. Hamblin. 1981. Theoretical aspects of selection for yield in stress and non-stress environments. *Crop Sci.* 21:943-946.
- Russell, W.A. 1974. comparative performance for maize hybrids representing different eras of maize breedings. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 29:81-101.
- . 1984. Agronomic performance of maize cultivars representing different eras of maize breeding. *Maydica* 29:375-390.
- . 1985a. Evaluations for plant, ear, and grain traits of maize cultivars representing seven eras of maize breeding. *Maydica* 30:85-96.
- . 1985b. Comparison of the hybrid performance of maize inbred lines developed from the original and improved cycles of BSSS. *Maydica* 30:407-419.
- . 1986. Contribution of breeding to maize improvement in the United States, 1920's-1980's. *Iowa State J. Res.* 61:5-34.

- , and S.A. Eberhart. 1968. Testcrosses of one- and two-ear types of corn belt maize inbreds. II. Stability of performance in different environments. *Crop Sci.* 8:248-251.
- , and -----, 1975. Hybrid performance of selected maize lines from reciprocal recurrent and testcross selection programs. *Crop Sci.* 15:1-4.
- , -----, and U.A. Vega. 1973. Recurrent selection for specific combining ability in two maize populations. *Crop Sci.* 13:257-261.
- , G.D. Lawrance, and W.D. Guthrie. 1979. Effects of recurrent selection for European corn borer resistance on other agronomic characters in synthetic cultivars of maize. *Maydica* 24:33-47.
- , and Veronica Machado. 1978. Selection procedures in the development of maize inbred lines and the effects of plant densities on the relationships between inbred traits and hybrid yields. *Iowa Agric. Home Econ. Exp. Stn. Res. Bull.* 585.
- , and C.L. Prior. 1975. Stability of yield performance of nonprolific and prolific maize hybrids. *Iowa State J. Res.* 50:17-27.
- , G.F. Sprague, and L.H. Penny. 1963. Mutations affecting quantitative characters in long-time inbred lines of maize. *Crop Sci.* 3:175-178.
- , and A.H. Teich. 1967. Selection in *Zea mays* L. by inbred line appearance and testcross performance in low and high plant densities. *Iowa Agric. Home Econ. Exp. Stn. Res. Bull.* 552.
- , and U.A. Vega. 1973. Genetic stability of quantitative characters in successive generations in maize inbred lines. *Euphytica* 22:172-180.
- Salazar, A.M., and A.R. Hallauer. 1986. Divergent mass selection for ear length in maize. *Rev. Bras. Genet.* 9:281-294.
- Schnell, F.W., and I.S. Singh. 1978. Epistasis in three-way crosses involving early flint and dent inbred lines of maize. *Maydica* 23:233-238.
- Scott, G.E. 1967. Selecting for stability of yield in maize. *Crop Sci.* 7:549-551.
- Shulka, G.K. 1972. Some statistical aspects of partitioning genotype-environment components of variability. *Heredity* 29:237-245.
- Shull, G.H. 1908. The composition of a field of maize. *Am. Breeders' Assoc. Rep.* 4:296-301.
- , 1909. A pure-line method in corn breeding. *Am. Breeders' Assoc. Rep.* 5:51-59.
- , 1910. Hybridization methods in corn breeding. *Am. Breeders' Mag.* 1:98-107.
- Silva, J.C., and A.R. Hallauer. 1975. Estimation of epistatic variance in Iowa Stiff Stalk Synthetic maize. *J. Hered.* 66:290-296.
- Singh, M. A.S. Khehra, and B.S. Dhillon. 1986. Direct and correlated response to recurrent full-sib selection for prolificacy in maize. *Crop Sci.* 26:275-278.
- Smith, H.F. 1936. A discriminant function for plant selection. *Ann. Eugen.* 7:240-250.
- Smith, J.S.C. 1988. Diversity of United States hybrid maize germplasm: Isozymic and chromatographic evidence. *Crop Sci.* 28:63-69.
- Smith, O.S. 1979a. A model for evaluating progress from recurrent selection. *Crop Sci.* 19:223-226.
- , 1979b. Application of a modified diallel analysis to evaluate recurrent selection for grain yield in maize. *Crop Sci.* 19:819-822.
- , 1983. Evaluation of recurrent selection in BSSS, BSCB1, and BS13 maize populations. *Crop Sci.* 13:35-40.
- , 1984. Comparison of effects of reciprocal recurrent selection in the BSSS(R), BSCB1(R), and BS6 populations. *Maydica* 29:1-8.
- , 1986. Covariance between line per se and testcross performance. *Crop Sci.* 26:540-543.
- , A.R. Hallauer, and W.A. Russell. 1981a. Use of selection index in recurrent selection programs in maize. *Euphytica* 30:611-618.
- , A.R. Hallauer, W.A. Russell, and T.M. Crosbie. 1981b. Use of selection indices in maize improvement and hybrid development programs. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 36:95-103.
- Sprague, G.F. 1946. Early testing of inbred lines. *J. Am. Soc. Agron.* 38:108-117.
- , 1952. Additional studies of the relative effectiveness of two systems of selection for oil content of the corn kernel. *Agron. J.* 44:329-331.
- , 1953. Heterosis. p. 113-136. *In* W.E. Loomis (ed.) *Growth and differentiation in plants*. Iowa State Univ. Press, Ames.
- , 1955. Corn breeding. p. 221-292. *In* G.F. Sprague (ed.) *Corn and corn improvement*. Academic Press, New York.

- , and B. Brimhall. 1950. Relative effectiveness of two systems of selection for oil content of the corn kernel. *Agron. J.* 42:83–88.
- , and S.A. Eberhart. 1977. Corn breeding. In G.F. Sprague (ed.) *Corn and corn improvement* 2nd ed. Agronomy 18:305–363.
- , and W.T. Federer. 1951. A comparison of variance components in corn yield trials. II. Error, year $\times$ variety, location $\times$ variety, and variety components. *Agron. J.* 43:535–541.
- , W.A. Russell, and L.H. Penny. 1960. Mutations affecting quantitative traits in the selfed progeny of doubled monoploid stocks. *Genetics* 45:855–866.
- , ———, ———, T.W. Horner, and W.D. Hanson. 1962. Effect of epistasis on grain yield in maize. *Crop Sci.* 2:205–208.
- , and L.A. Tatum. 1942. General vs. specific combining ability in single crosses of corn. *J. Am. Soc. Agron.* 34:923–932.
- , and W.I. Thomas. 1967. Further evidence of epistasis in single and three-way cross yields of maize (*Zea mays* L.). *Crop Sci.* 7:355–356.
- St. Martin, S.K., P.J. Loesch, Jr., J.T. Demopulos-Rodriguez, and W.S. Wiser. 1982. Selection indices for the improvement of opaque-2 maize. *Crop Sci.* 22:478–485.
- Stadler, L.J. 1944. Gamete selection in corn breeding. *J. Am. Soc. Agron.* 36:988–989.
- Stangland, G.R., and W.A. Russell. 1981. Variability within S_2 and S_8 inbred lines of maize. *Maydica* 24:227–238.
- , ———, and O.S. Smith. 1982. Agronomic evaluation of four maize synthetics and their crosses after recurrent selection for yield. *Maydica* 27:199–1212.
- Stringfield, G.H. 1974. Developing heterozygous parent stocks for maize hybrids. DeKalb AgResearch, DeKalb, IL.
- Stuber, C.W., W.P. Williams, and R.H. Moll. 1973. Epistasis in maize (*Zea mays* L.). III. Significance in predictions of hybrid performance. *Crop Sci.* 13:195–200.
- Subandi, W., A. Compton, and L.T. Empig. 1973. Comparison of the efficiencies of selection indices for three traits in two variety crosses of corn. *Crop Sci.* 13:184–186.
- Suwantaradon, K., S.A. Eberhart, J.J. Mock, J.C. Owens, and W.D. Guthrie. 1975. Index selection for several agronomic traits in the BSSS maize population. *Crop Sci.* 15:827–833.
- Tai, G.C.C. 1971. Genotypic stability analysis and its application to potato regional trials. *Crop Sci.* 11:184–190.
- Tallis, G.M. 1962. A selection index for optimum genotype. *Biometrics* 18:120–122.
- Tanner, A.H., and O.S. Smith. 1987. Comparison of half-sib and S_1 recurrent selection in Krug Yellow Dent maize populations. *Crop Sci.* 27:509–513.
- Tapper, D.C. 1983. Changes in physiological traits associated with grain yield improvement in single-cross maize hybrids from 1930 to 1970. Ph.D. diss. Iowa State Univ., Ames. (Diss. Abstr. 83-DA8316164).
- Thompson, D.L. 1954. Combining ability of homozygous diploids of corn relative to lines derived by inbreeding. *Agron. J.* 46:133–136.
- Thompson, L.N. 1975. Weather variability, climatic changes, and grain production. *Science*. 188:535–541.
- . 1986. Climatic change, weather variability, and corn production. *Agron. J.* 78:649–653.
- Trifunovic, V. 1978. Maize production and maize breeding in Europe. p. 41–58. In D.B. Walden (ed.) *Maize breeding and genetics*. John Wiley and Sons, New York.
- Troyer, A.F., and W.L. Brown. 1972. Selection for early flowering in corn. *Crop Sci.* 12:301–304.
- Tsotsis, B. 1972. Objectives of industry breeders to make efficient and significant advances in the future. *Proc. Annu. Corn Sorghum Ind. Res. Conf.* 27:93–107.
- Walejko, R.N., and W.A. Russell. 1977. Evaluation of recurrent selection for specific combining ability in two open-pollinated maize cultivars. *Crop Sci.* 17:647–651.
- Weatherspoon, J.H. 1970. Comparative yields of single, three-way, and double crosses of maize. *Crop Sci.* 10:157–159.
- Wellhausen, E.J. 1978. Recent developments in maize breeding in the tropics. p. 59–84. In D.B. Walden (ed.) *Maize breeding and genetics*. John Wiley and Sons, New York.
- West, D.R., W.A. Compton, and M.A. Thomas. 1980. Comparison of replicated S_1 per se vs. reciprocal full-sib index selection in corn. I. Indirect response to population densities. *Crop Sci.* 20:35–42.

- Westcott, B. 1986. Some methods of analyzing genotype-environment interaction. *Heredity* 56:243-253.
- Widstrom, N.W. 1974. Selection indexes for resistance to corn earworm based on realized gains in corn. *Crop Sci.* 14:673-675.
- , B.R. Wiseman, and W.W. McMillan. 1982. Responses to index selection in maize for resistance to ear damage by corn earworm. *Crop Sci.* 22:843-846.
- Williams, J.S. 1962. The evaluation of a selection index. *Biometrics* 18:375-393.
- Williams, P.N., and F.M. Davis. 1983. Recurrent selection for resistance in corn to tunneling by the second-brood southwestern corn borer. *Crop Sci.* 23:169-170.
- Wricke, G. 1962. Über eine methode zur erfassung der ökologischen streubreite in feldversuchen. *Z. Pflanzenzuecht.* 47:92-96.
- Wright, A.J. 1971. The analysis and prediction of some two factor interactions in grass breeding. *J. Agric. Sci.* 76:301-306.
- . 1976. Bias in the estimation of regression coefficients in the analysis of genotype-environmental interaction. *Heredity* 37:299-303.
- . 1980. The expected frequencies of half-sib, testcross, and S_1 progeny testing methods in single population improvement. *Heredity* 45:361-376.
- Yates, F., and W.G. Cochran. 1938. The analysis of groups of experiments. *J. Agric. Sci.* 28:556-580.
- Zambezi, B.T., E.S. Horner, and F.G. Martin. 1986. Inbred lines as testers for general combining ability in maize. *Crop Sci.* 26:908-910.
- Zhang, Q., and S. Geng. 1986. A method for estimating varietal stability for data of long-term trials. *Theor. Appl. Genet.* 71:810-814.
- Zuber, M.S., and L.L. Darrah. 1980. 1979 U.S. corn germplasm base. *Proc. Ann. Corn Sorghum Ind. Res. Conf.* 35:234-249.