

Long-term Selection in a Commercial Hybrid Maize Breeding Program

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I. INTRODUCTION

A. Utility of Studying Long-term Commercial Breeding Programs

Commercial plant breeders have the same goal as plant breeders in the public sector—to produce improved cultivars that suit the needs of farmers who plant them. But commercial breeding differs from public sector breeding in at least one respect: retrospective analyses of long-term commercial breeding programs are seldom published in the scientific literature. Job security for a commercial breeder depends on production of successful cultivars, not on production of peer-reviewed publications. However, both private and public plant breeders could benefit from such reports. The reports could show the consequences (intended or unintended) of specific breeding and selection programs, measure rates of gain for important traits such as yield or pest resistance, and identify and quantify useful sources of and changes in genetic diversity. Such information and analysis could help breeders to refine and/or change their breeding programs in desired directions and to make qualified estimates of future progress.

B. A Long-term Selection Program in the Private Sector: 1930s to 2000s

This report will summarize the findings of a series of studies (Duvick 1977, 1984, 1992, 1997; Duvick et al. 2003) of a long-term commercial plant-breeding program—a “long-term selection experiment.” The studies compare field performance, parental origins, and genotype changes for a time-series of maize hybrids (see Table 4.1, “Era hybrids”) that have been released sequentially in the West-central U.S. Corn Belt during the past seven decades—from the early 1930s through 2001. Each hybrid was successful and widely grown in its time. All of the hybrids were bred, produced, and sold by Pioneer Hi-Bred International. This constantly lengthening series of hybrids has been grown in side-by-side per-

Table 4.1. List of Era hybrids and year of hybrid release. Open pollinated cultivars included in the list arbitrarily are classified as 1930, a year in which they were widely grown and well regarded.

Cultivar	Year	Cultivar	Year	Cultivar	Year
RYD1 ^z	1930	329	1954	3378	1983
BYD	1930	354A	1958	3475	1984
KYD	1930	328	1959	3379	1988
RYD2	1930	3618	1961	3362	1989
351 ^y	1934	3206	1962	3417	1990
307	1936	3306	1963	3394	1991
322	1936	3376	1965	3563	1991
317	1937	3390	1967	3279	1992
330	1939	3571	1968	3489	1994
336	1940	3334	1969	3335	1995
340	1941	3388	1970	34G81	1997
339	1942	3517	1971	33A14	1997
344	1945	3366	1972	33G26	1998
352	1946	3301A	1974	34B23	1999
350B	1948	3529	1975	33P66	1999
347	1950	3541	1975	33P67	1999
301B	1952	3382	1976	34G13	2000
354	1953	3377	1982	34M95	2001
				33R77	2001

^zRYD1 = Neal Reid Yellow Dent; BYD = Black Yellow Dent; KYD = Krug Yellow Dent; RYD2 = Reid Yellow Dent. BYD, KYD and RYD obtained from USDA Plant Introduction Station, Ames, IA. RYD1 obtained from Iowa farmer, Neal.

^yNumerical description of hybrids.

formance trials annually during the past 25 years, and was also subjected to other phenotypic and genotypic measurements. From time to time the accumulated data have been summarized, analyzed, and published. We will review pertinent comments and data from those published reports and also present new data relative to this “long-term selection experiment.”

1. Intended Breeding Goals. Higher grain yield has been the Pioneer breeders’ avowed primary breeding goal over the decades, but from time to time various biotic and abiotic problems have necessitated the urgent implementation of additional goals. For example:

Severe drought during the early years of the 1930s pushed selection in the direction of drought tolerance, but the occurrence of ear smut [*Ustilago zae* (Beckm.) Unger] in some of the

drought-tolerant germplasm then necessitated selection for resistance to smut.

The onset of European corn borer [*Ostrinia nubilalis* (Hübner)] in the 1950s brought new needs for insect tolerance.

Farmer use of higher plant densities and increased rates of nitrogen fertilizer, starting in the 1960s, increased needs for hybrids with stronger roots and stalks, and greater resistance to barrenness.

Plant density continues to increase to this day, even though nitrogen application amounts have leveled off. Constantly increasing plant density constantly increases needs for drought and shading tolerance, as well as for other kinds of stress tolerance.

In recent years no-till and minimum-till planting have increased the need for hybrids with tolerance to new diseases such as gray leaf spot (*Cercospora zeae-maydis* Tehon & E.Y. Daniels).

Thus, one might say that the breeders' constant goal has been to develop hybrids that produce higher yields in spite of a constantly enlarging array of biotic and abiotic stresses. The stresses were brought on in part by changing cultural techniques and in part by the increasingly monoculture nature of maize production in the U.S. Corn Belt.

2. Starting Materials. Open pollinated cultivars (OPCs), such as 'Reid Yellow Dent' and 'Krug', provided germplasm for the first round of inbred development (started in the 1920s) and subsequent hybrid production. The OPCs usually were chosen because of superior performance in yield trials such as those conducted by Iowa State College, or because they were highly regarded by farmers. Crosses among some (but not all) of these first inbreds were the foundation of the next cycle of selfing and inbred production. Those inbreds were supplemented by a few new inbreds that had been developed from additional OPCs. Later cycles of inbred production continued this pattern of recycling currently successful inbreds while also incorporating germplasm of a few new inbreds from other sources. In the early decades, public inbred lines such as WF9 and M14 significantly contributed to pedigrees of the Era hybrids. They supplemented the small number of inbreds that had been developed by the initially small number of Pioneer breeders (one breeder for the entire company, in the beginning). But over the decades the proportion of Pioneer-bred inbred lines increased continually to the point that no public inbreds were used directly in any of the hybrids. During the past

two decades, all inbreds in Era hybrids have been Pioneer-bred. However, some of the important public inbred lines from earlier decades (e.g., Oh43, B37, B73) were progenitors of highly useful inbred lines as developed by Pioneer breeders. Details of this evolutionary history will be shown in later sections of this account.

3. Breeding Methods, Breeders. Pedigree breeding—to develop new inbreds by selfing crosses of proven inbred lines—has been the primary means of developing new inbreds during the seven decades of breeding Era hybrids. Improved populations occasionally have produced successful inbred lines or (more frequently) contributed as a parent when crossed to one or more successful inbred lines. A small number of outstandingly important inbred lines have come from synthetic populations (e.g., the public inbreds B37 and B73 from BSSS, the Iowa Stiff Stalk Synthetic). But the great majority of the inbreds in the Era hybrids were developed by means of pedigree breeding at the hands of Pioneer breeders.

During the past 70 years, many breeders have contributed to development of the Era hybrids, despite the small number of breeders in the beginning. Collectively, they have encompassed a wide range of education and experience and, consequently, they have differed in how they practiced the art and science of plant breeding. The composition of the group has changed continually over the seven decades of this long-term selection program. The first breeders had little or no training in plant breeding and genetics but their replacements had more training in these fields and eventually all breeders had advanced degrees in plant breeding or allied fields of science. Not more than two or three breeders at a time were directly responsible for making and testing inbreds and hybrids for central Iowa (the adaptation region of the Era hybrids). However, Pioneer breeders from other parts of the U.S. Corn Belt have contributed numerous inbred lines or hybrids (especially in the later decades) that ended up in one or more Era hybrids.

The one consistent feature of the plant breeding group was its pragmatism. If a method or source of germplasm worked, it was used whether or not it fit the current styles in breeding theory. All newly proposed theoretical approaches were tried thoroughly, although not at the expense of practical techniques that were producing good results. If the new approaches worked, they were used; if they proved to be unproductive after thorough testing, they were discontinued. The net result (as noted above) has been that over the years the breeders primarily, but not exclusively, have relied on pedigree breeding. It has been the most

dependable method for producing improved inbred lines. Germplasm for the most part came from inbred lines that had proven their utility in commercial hybrids. Widespread on-farm performance of released hybrids was used to identify the top-performing inbreds, to winnow the best from merely average germplasm.

Over the years the pedigree breeding effort has evolved from a structure analogous to a single population improvement program to a two-population improvement program. With the formation of the current Stiff Stalk (SS) and Non Stiff Stalk (NSS) heterotic groups of germplasm (e.g., Casa et al. 2002), this breeding approach can be considered to be an open reciprocal recurrent selection (RRS) strategy, with pedigree breeding being undertaken within both the SS and NSS heterotic groups. These groups can be further divided into sub-groups and heterosis is evident among some of these sub-groups. New inbreds developed within one heterotic group are evaluated on their testcross performance in multi-environment trials, with testers being drawn from one or more pools of elite inbreds drawn from a complementary heterotic group.

II. RESULTS

A. Performance Trials

1. Commercial Hybrids

Grain Yield. Previous studies of the Era hybrids consistently have shown linear increases in grain yield, from oldest to newest hybrids (Duvick 1977, 1984, 1992, 1997; Duvick et al. 2003). Genetic yield gain has been continual and constant in amount (on average) over the years. The studies also consistently show that the oldest hybrids make their maximum yields at lower plant densities typical of maize farming in the early decades, whereas the newer hybrids yield the most at higher plant densities typical of recent decades. Plant densities in the 1930s were ca. 30 thousand plants/ha. Planting rates have gradually increased until today in central Iowa plant densities are ca. 75 thousand plants/ha or higher.

In contrast to annual increases in yield per unit area, the reports show that yield potential per plant (maximum possible grain yield per plant) has not increased appreciably over the years. That is, the oldest hybrids yield nearly as much as the newest hybrids when plants are widely spaced (10 thousand plants/ha), have minimal levels of biotic and abiotic stress, and, consequently, are able to maximize the yield on individual plants. This result shows that increases in yield per unit area of

the newer hybrids are owed not to increased yield potential per plant but, rather, to the hybrids' ability to produce a minimum amount of grain (about 0.15 kg) on every plant when they are grown at higher plant densities. At today's higher plant densities, the older hybrids typically have a high percentage of barren plants, or ears with very few kernels, whereas the new hybrids have an ear on every plant.

The yield data from recent years agree with the previous results. Trials of Era hybrids (listed in Table 4.1) conducted during the past 10 years (1991 to 2001) show that the annual genetic yield gain is still linear, averaging 77 kg/ha (Fig. 4.1). Fig. 4.1 shows the yield of each hybrid at the plant density in which it made the highest yield. (The hybrids were compared in split-plot trials at 30, 54, and 79 thousand plants/ha.) Use of the "optimum plant density" yield gives a more realistic measurement of genetic yield gain, as compared with measurements at any single plant

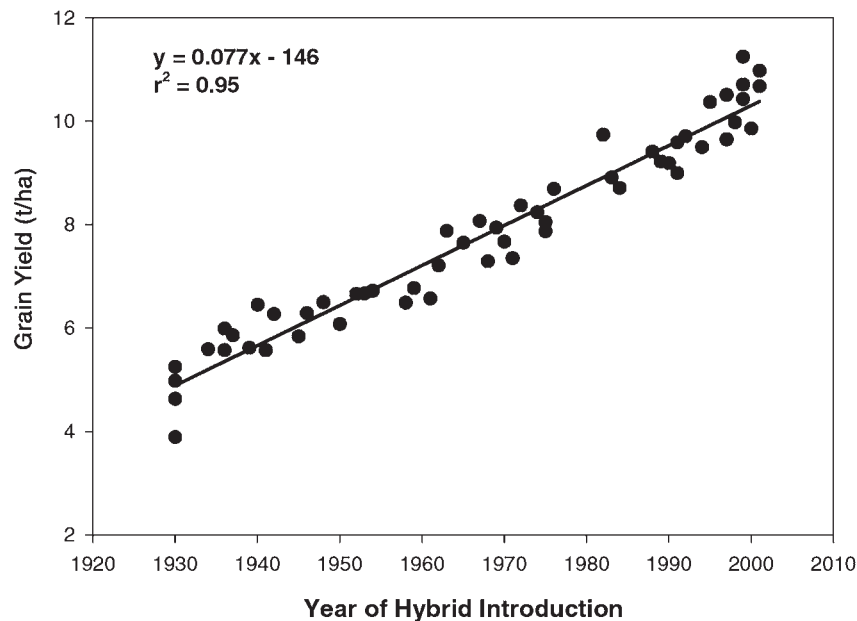


Fig. 4.1. Grain yield per hybrid regressed on year of hybrid introduction. Best Linear Unbiased Predictors (BLUPs) of hybrid grain yield based on trials grown in the years 1991 to 2001, at three locations per year in central Iowa, at three densities (30, 54, and 79 thousand plants/ha), one replication per density. Yield per hybrid is for the density giving the highest average yield.

density, because each hybrid is evaluated at a reasonably close approximation of the plant density at which it was bred and tested. As noted earlier, usually the older hybrids yield most at lower plant densities and the newer hybrids yield most at higher plant densities.

Recent yield data also agree with those from earlier years (and thus shorter time-series) in showing a strong interaction between hybrid age and plant density in regard to their effects on grain yield (Fig. 4.2). Fig. 4.2 summarizes the 1991 to 2001 data for Era hybrids when grown at three widely different plant densities: ca. 10, 30, and 79 thousand plants/ha. (The 10 thousand plants/ha density was planted alongside the 3-density split-plot trial, essentially giving a split-split-plot trial. It was intended to measure potential yield per plant at minimal levels of stress.) Fig. 4.2 demonstrates clearly that although genetic yield gain over the years is linear and positive at all three plant densities, the gain is minimal or nil at 10 thousand plants/ha and maximal at 79 thousand plants/ha.

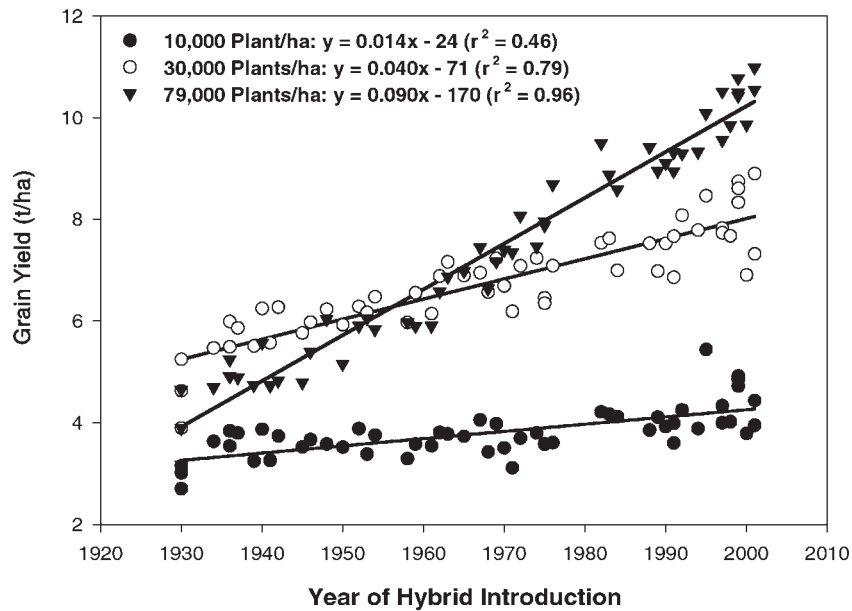


Fig. 4.2. Grain yield per hybrid regressed on year of hybrid introduction at each of three plant densities (10, 30, and 79 thousand plants/ha). Best Linear Unbiased Predictors (BLUPs) for hybrid grain yield based on trials grown in the years 1991 to 2001, three locations per year, one replication per density.

Yield gains for the time-series were nearly as great in low-yield (i.e., high stress) seasons as in high-yield (i.e., low stress) seasons. For example, trends were linear and similar in amount in three widely different seasons (Fig. 4.3). The seasons are described as follows:

1992: Exceptionally high yields because of a “nearly perfect” growing season. Statewide yields in 1992 were at record highs.

1993: Low yields because of waterlogged soil and cool temperatures during most of the growing season. (“The Year of the Floods,” was one of the coolest and wettest growing seasons on record for Iowa.)

2001: Low yields because of a season-long local drought, especially severe at the sensitive anthesis-silking period.

The newer hybrids outyielded the older hybrids in low-yield as well as in high-yield environments, not only between seasons but also within

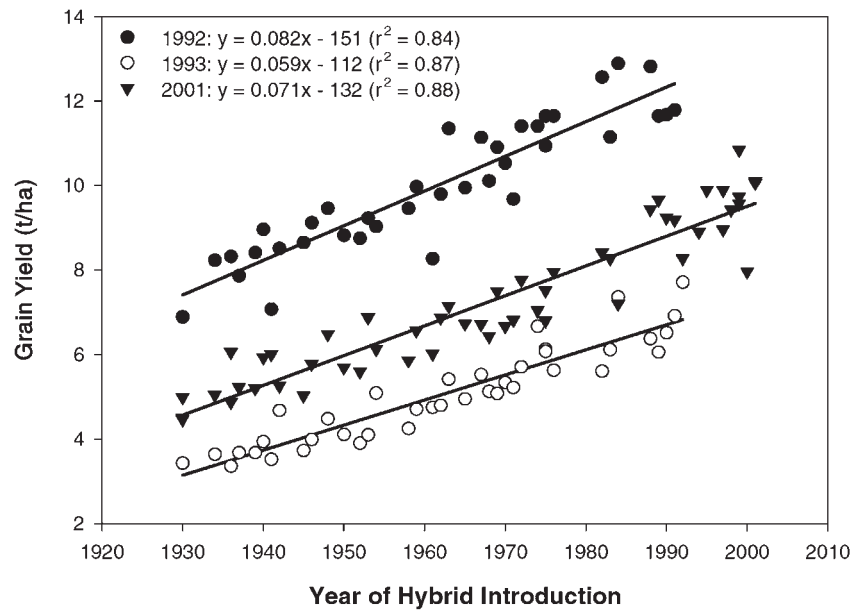


Fig. 4.3. Grain yield per hybrid regressed on year of hybrid introduction for trials grown in 1992, 1993, and 2001. Yield per hybrid is for the density giving the highest average yield.

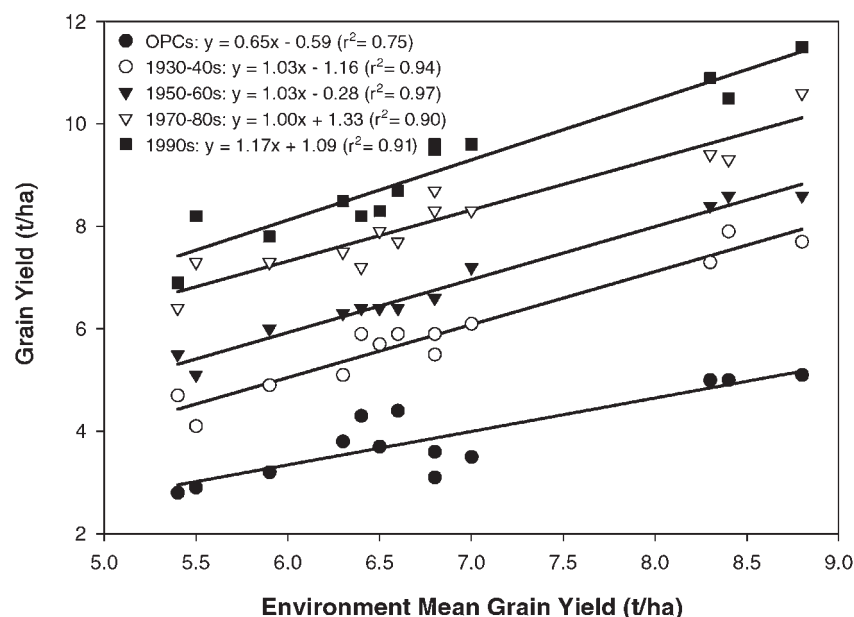


Fig. 4.4. Mean grain yield of hybrids released within two-decade spans, and of three OPCs, regressed on mean yield of all hybrids per environment. Trials grown in a total of 13 environments during the years 1996 through 2000. Means of three plant densities per environment (30, 54, and 79 thousand plants/ha).

seasons. When hybrids are aggregated by double-decade of release (1930s plus 1940s, etc., with OPCs in a class by themselves), the newer the class of hybrids the higher the yield, in low-yield as well as high-yield trial locations (Fig. 4.4). Data are from 13 locations, accumulated over the years 1996 to 2000.

Other Traits. Table 4.2 summarizes various observations that have been made from time to time on additional traits of the Era hybrids. Several of these traits have changed over the years. The changes can be sorted arbitrarily into two groups: (1) changes that add efficiency to the maize plant's grain production process, and (2) changes that improve or give evidence for improvement in stress tolerance and thus improve chances for good yields in stressful growing conditions. (We emphasize that this is an arbitrary classification and note that to list a trait in one category does not imply that it cannot also have some effect in the alternate category; for example, efficiencies from reduced tassel size could well increase stress tolerance in regard to grain production.)

Table 4.2. Linear regressions (b) of trait on year of introduction of Era hybrids introduced from 1934 to 2001. Regressions include some or all of the hybrids in Table 4.1, depending on the year in which measurements were taken. The data for all of the 1991 to 2001 summaries (based on Best Linear Unbiased Predictors), and for leaves per plant, fodder weight, harvest index, and mean value per trait are reported herein for the first time. All other data are from Table 2 of Duvick 1997.

Trait change/stability	Trial years	Density (000 ha ⁻¹)	b (10 yr ⁻¹)	R ²	Trait mean
Change, Efficiency					
Tassel weight	1992	30,54,79	-0.5 g	0.70	3.5
Tassel branch number	1992	30,54,79	-2.5 branch	0.66	15.5
Tassel size score ^z	1991–2001	30,54,79	-0.9 score	0.91	5.4
Grain protein (%)	1992	30,54,79	-0.3%	0.68	9.8
Grain starch (%)	1992	30,54,79	+0.3%	0.56	70.4
Leaf angle score	1991–2001	30,54,79	+1.0 score	0.81	4.7
Non-tillered plants (NT) (%)	1992, 1994	30,54,79	+4% NT	0.48	86.4
Change, Stress tolerance					
ASI	1991–2001	30,54,79	-13 GDU	0.81	48
Ears per 100 plants	1991–2001	30,54,79	+3.6 ears	0.78	92.9
Staygreen score	1991–2001	30,54,79	+0.6 score	0.75	5.1
Not stalk-lodged (%)	1991–2001	30,54,79	+1.6%	0.69	91.3
Not root-lodged (%)	1991–2001	30,54,79	+4.1%	0.67	81.5
ECB2 tunnel length	1992	30,54,79	-1.5 cm	0.46	9.9
ECB2 damage score	1992, 1994	30,54,79	+0.5 score	0.58	2.9
NLB tolerance score	1994	30,54,79	+0.7 score	0.34	4.3
Stability, Intentional					
Plant height	1991–2001	30,54,79	-1 cm	0.11	270
Ear height	1991–2001	30,54,79	-3 cm	0.40	116
50% anthesis, GDU	1991–2001	30,54,79	+4 GDU	0.07	1412
Grain moisture (%)	1991–2001	30,54,79	+0.1%	0.05	21.88
Stability, Unintentional					
Leaves per plant	1992	30,54,79	+0.1	0.05	13.3
Fodder weight per plant	1985	30,54,69	+3 g	0.01	220
Harvest Index (%)	1985	30,54,69	+1.0	0.45	40
Rows per ear	1992	30,54,79	-0.5 rows	0.36	16.7
Kernels per row	1992	30,54,79	+0.4 k/row	0.06	40.2
Kernels per ear	1992	30,54,79	-11 kernels	0.11	670
100 kernel weight	1992	30,54,79	+0.7 g	0.31	31.7
Test wt. since 1955	1991–2001	30,54,79	+8.7 kg m ⁻³	0.65	704
Grain oil (%)	1992	30,54,79	-0.0%	0.07	4.5
ECB1 leaf feed score	1994	30,54,79	+0.3 score	0.19	2.6
Heterosis (SX-MP)					
Plant height	1992–1993	30,54,79	-9 cm	0.26	+193
50% Anthesis	1992–1993	30,54,79	-0.3 GDU	0.00	-117
Grain Yield (t/ha)	1992–1993	30,54,79	+0.1 t/ha	0.01	+4.3

^zTassel size score: 1 to 9, 9 = largest size; Leaf angle score: 1 to 9, 9 = most upright; ASI: anthesis-silking interval; GDU: growing degree units, °C; Staygreen score: 1–9, 9 = least premature senescence; ECB2: European corn borer, 2nd generation; ECB2 damage score: 1–9, 9 = least damage; Harvest index: grain to fodder ratio; ECB1: European corn borer, 1st generation; ECB1 leaf feeding score: 1–9, 9 = least leaf feeding; NLB: Northern leaf blight; NLB Score: 1–9, 9 = most tolerant; SX-MP = single cross minus mid-parent mean.

Some traits have not changed, or the amount of change has been non-significant—the traits have been relatively stable over the years. These “stable” traits also can be sorted into two groups: (a) stability enforced by way of breeders’ selection (such as a ceiling on grain moisture at harvest time) and (b) stability in absence of breeder attention (or in some cases, stability despite breeders’ hope for change).

Changes that increase efficiency of grain production are: smaller tassels (more energy available for grain production, and less shading of the leaves); reduced grain protein percentage and increased grain starch percentage (less energy is required to make starch than to make protein); more upright leaves (better light interception in dense plantings); and fewer tillers (assuming that tillers without ears use water and nutrients that otherwise would be available for grain production).

Changes that demonstrate or provide greater stress tolerance are: shorter anthesis-silking interval (an indication that ear development is not hindered); more ears per 100 plants (fewer barren plants at higher plant densities or in other stressful environments, and more two-eared plants at lower plant densities and in more favorable environments); higher staygreen score (plants are less prone to premature death); less stalk lodging (stronger stalks with better resistance to stalk rot organisms); less root lodging (better ability to maintain erect plants when strong winds follow heavy rainfall); less tunneling and less visible damage by second generation European corn borer (increased genetic resistance to the insect); and slight trend to improvement in tolerance to northern corn leaf blight [*Exserohilum turcicum* (Pass.) K. J. Leonard & E.G. Suggs].

As noted earlier, breeders deliberately selected for no change in certain traits. Such intentionally stable traits were: plant height and ear height (essentially no change in plant height over the years to satisfy farmers’ antipathy to overly-tall plants, and only minimal reductions in ear height); and hybrid maturity (time of anthesis and grain moisture at harvest were unchanged during 70 years of breeding and selection, to ensure ripening of the grain before average date of first frost).

Other traits also did not change materially, even though breeders did not directly select for stability. Hybrids showed little or no change in: plant size as measured by leaves per plant, leaf area, and fodder weight (no change over the years); harvest index (very little improvement as averaged over plant densities, although there is a trend to higher harvest index as plant densities are increased); rows per ear, kernels per row, kernels per ear, and 100-kernel weight (little or no change, although there is a slight trend to fewer and larger kernels); test weight (increased consistently since 1955 but the average annual increase has been small—

about 0.1% per year); grain oil percentage (unchanged over the years); tolerance to leaf feeding of first generation European corn borer (no improvement); and heterosis (no substantial increase on average during the period 1930s through 1980s, as measured for plant height, flowering date, and grain yield. Heterosis is calculated as value of a single-cross mean minus that of its mid-parent mean. See section IIA2, for further discussion of heterosis effects.)

Genotypic and Genotype-by-Environment Interactions. When examining genetic gain for traits in a target population of environments, it is important to consider the relative influences of different sources of genotype-by-environment interactions. Here we were interested in the relative sizes of the variance components for genotypic variance, genotype interactions with the important management variable plant density, and genotype interactions with the range of environments that were sampled at different year-location combinations in the Era experiments.

Analyses of variance were conducted for grain yield and agronomic traits using the data from the Era experiments conducted from 1991 to 2001. To accommodate the inherent imbalance that is introduced into the data set when new hybrids are added sequentially over years, the results of the experiments were analyzed as a mixed-model. Environments (year-location combinations) and hybrids were treated as random effects and plant density as a fixed effect. Since the Era experiments are conducted as single replicates for each year-location combination, the residual term in the analysis is a combination of the hybrid-by-environment-by-plant density interaction and experimental error. The trait performance of the hybrids was computed as a Best Linear Unbiased Predictor (BLUP). All analyses were conducted using the ASREML software (Gilmour et al. 1998). The mixed model enabled estimation of components of variance for hybrids, hybrid-by-environment ($H \times E$) interaction and hybrid-by-plant density ($H \times D$) interaction. The variance components were used to obtain estimates of heritability for the traits to provide a measure of degree of genotypic determination for the phenotypic observations in the Era experiments. Analyses were conducted for the complete set of hybrids and also for sets of hybrids released in three time-periods (see Table 4.1):

- 1930 to 1959, representing the period when double-cross hybrids dominated
- 1960 to 1989, representing the period when the Stiff Stalk and Non Stiff Stalk pools of germplasm were formalized and single-cross hybrids appeared and dominated

1990 to 2001, representing the most modern germplasm consisting of single-cross hybrids combining inbreds from the Stiff Stalk and Non Stiff Stalk pools

Examined over the complete set, the genotypic (“Hybrid”) variation for grain yield and most agronomic traits was significantly larger than H×E and H×D sources of genotype-by-environment interaction (Table 4.3). Heritability estimates on a single environment or on multiple environment bases were moderate to large. As expected, for those traits where selection has resulted in direct or indirect changes, the genotypic variance component within the three time periods was smaller than when considered across the complete set of hybrids. The H×E and H×D interaction components of variance changed with time period and the pattern of change between the time periods differed among the traits. For grain yield the hybrid, H×E, and H×D variance components increased from the 1930 to 1959 time period to the 1960 to 1989 time period. The increases in these components of variance are indicative of the broadening of the genetic variation among the successful hybrids created by the Pioneer breeding program over these time periods. They also indicate the important influences of H×D and H×E interactions on the grain yield performance of the hybrids in the target population of environments. In the 1990 to 2001 time period, compared with the 1960 to 1989 time period, there was a slight reduction in the hybrid variance component (0.33 ± 0.14 cf. 0.43 ± 0.17) and a more noticeable reduction in the H×E interaction (0.07 ± 0.04 cf. 0.16 ± 0.03) and H×D interaction (0.01 ± 0.02 cf. 0.18 ± 0.05) components of variance. These trends suggest that the modern hybrids (1990 to 2001, Table 4.1) are all similarly adapted to the range of plant densities considered in the Era experiments and are more stable in their higher yield performance across environments than were the hybrids from the 1960 to 1989 time period.

The heritability estimates within the three time periods were usually lower than for the complete data set. These lower estimates of heritability (within the three time periods) are indicative of the more limited viewpoint that a corn breeder would have of the extent of genotypic variation among these hybrids and potential for further progress while working within a time period. This can be contrasted with the more obvious changes in the traits that can be observed over the whole period encompassed by the sequence of hybrids included in the Era study (Fig. 4.5).

Hybrid Yield at Time of Release versus Yield in Era Trials. Today’s agronomic practices, pest problems, and perhaps climatic conditions are different from those of earlier decades (e.g., in the 1930s), and therefore

Table 4.3. Estimates of Hybrid (genotypic), Hybrid-by-Environment (H×E), Hybrid-by-Density (H×D) and residual variance components ($\pm$ Standard Errors) and heritability ($h^2_{(1 \text{ env})}$) = on a single location, single density, single year basis; $h^2_{(9E,3D)}$ = on a line-mean across 9 environments and 3 density basis) for grain yield and agronomic traits based on available data from Era experiments conducted from 1991 to 2001. #Number, indicates the number of hybrids that were used to estimate the components of variance. (This number can differ among traits for a time period because some hybrids were not measured, particularly for the more recent hybrids.)

Trait	#Number	Set	Hybrid	H×E	H×D	Residual	$h^2_{(1 \text{ env})}$	$h^2_{(9E,3D)}$
Yield (t/ha)	55	All	2.65±0.55	0.19±0.02	0.48±0.07	0.69±0.02	0.66	0.93
	17	1930–1959	0.17±0.07	0.09±0.02	0.03±0.01	0.60±0.03	0.19	0.81
	19	1960–1989	0.43±0.17	0.16±0.03	0.18±0.05	0.68±0.03	0.29	0.81
	15	1990–2001	0.33±0.14	0.07±0.04	0.01±0.02	0.79±0.06	0.28	0.89
ASI (GDU)	55	All	11.7±2.4	1.7±0.2	0.8±0.2	7.2±0.3	0.55	0.94
	17	1930–1959	2.4±0.9	0.9±0.4	0.1±0.1	9.0±0.5	0.19	0.84
	19	1960–1989	4.7±1.7	1.3±0.3	0.5±0.2	5.9±0.3	0.38	0.90
	15	1990–2001	0.7±0.4	0.6±0.3	0.0±0.1	3.5±0.3	0.15	0.78
Staygreen (1–9 Score)	49	All	2.74±0.59	0.49±0.06	0.06±0.02	1.31±0.05	0.60	0.96
	17	1930–1959	0.71±0.27	0.37±0.08	0	1.23±0.08	0.31	0.89
	19	1960–1989	1.08±0.39	0.37±0.07	0.08±0.04	1.27±0.08	0.39	0.90
	9	1990–2001	0.57±0.40	0.26±0.15	0.11±0.11	1.15±0.17	0.27	0.84
Ear Number (ears/100 plants)	55	All	101.7±22.4	10.9±3.7	23.9±4.9	135.6±5.4	0.37	0.88
	17	1930–1959	0.5±4.0	17.8±5.3	16.9±5.9	97.6±6.6	0.00	0.04
	19	1960–1989	39.0±17.4	1.4±5.3	27.9±8.9	143.3±9.0	0.18	0.73
	15	1990–2001	10.7±11.2	5.0±9.2	23.8±12.1	142.6±14.8	0.06	0.44
Leaf Angle (1–9 Score)	55	All	6.17±1.20	0.19±0.03	0	1.09±0.04	0.83	0.99
	17	1930–1959	0.32±0.12	0.12±0.05	0	1.31±0.07	0.18	0.84
	19	1960–1989	2.64±0.89	0.23±0.05	0	1.16±0.06	0.66	0.97
	15	1990–2001	0.33±0.14	0.08±0.03	0	0.31±0.03	0.46	0.94

(continued)

Table 4.3. (Continued)

Trait	#Number	Set	Hybrid	H×E	H×D	Residual	$h^2_{(1\text{ env})}$	$h^2_{(9E,3D)}$
Tassel Size (1–9 Score)	55	All	4.89±0.95	0.19±0.03	0.02±0.01	0.79±0.03	0.83	0.99
	17	1930–1959	0.93±0.34	0.09±0.04	0.03±0.02	0.95±0.06	0.46	0.94
	19	1960–1989	1.43±0.49	0.22±0.04	0.01±0.01	0.85±0.05	0.57	0.96
	15	1990–2001	0.28±0.12	0.12±0.04	0.01±0.01	0.41±0.04	0.35	0.90
Moisture (%)	55	All	2.42±0.49	1.01±0.06	0.11±0.03	1.68±0.05	0.46	0.92
	17	1930–1959	1.27±0.47	0.49±0.07	0.09±0.03	1.42±0.07	0.39	0.90
	19	1960–1989	3.02±1.03	1.10±0.09	0.10±0.03	1.23±0.05	0.55	0.94
	15	1990–2001	2.60±1.06	0.80±0.14	0.18±0.09	1.36±0.11	0.53	0.93
Ear Height (cm)	53	All	66.2±14.0	8.6±2.8	2.3±1.3	118.6±4.2	0.34	0.92
	17	1930–1959	23.7±10.1	10.8±5.1	5.5±3.1	129.5±7.6	0.14	0.75
	19	1960–1989	51.4±17.7	4.1±3.3	0	98.1±5.2	0.33	0.93
	13	1990–2001	53.3±24.8	5.8±6.3	2.4±3.5	89.5±9.4	0.35	0.92
Plant Height (cm)	53	All	57.8±12.8	9.6±4.0	3.3±2.0	179.4±6.3	0.23	0.87
	17	1930–1959	11.3±6.1	0	4.0±4.2	247.4±11.8	0.04	0.52
	19	1960–1989	66.9±23.3	13.6±4.40	1.2±1.7	112.4±6.1	0.34	0.92
	13	1990–2001	68.1±35.5	27.3±13.5	2.4±5.1	156.9±16.5	0.27	0.88
% Not Root Lodged	53	All	149.5±33.8	84.9±11.3	4.8±4.0	200.6±10.1	0.34	0.89
	17	1930–1959	30.5±16.4	58.0±16.5	6.3±7.2	213.6±18.0	0.10	0.65
	19	1960–1989	7.9±6.1	41.1±12.0	0	178.8±13.3	0.03	0.42
	13	1990–2001	0.3±1.0	0	0	35.1±3.7	0.01	0.17
% Not Stalk Lodged	55	All	23.4±5.1	12.3±1.9	0	60.0±2.2	0.24	0.87
	17	1930–1959	12.1±5.1	10.9±3.8	0	85.5±5.1	0.11	0.73
	19	1960–1989	3.9±1.9	10.8±2.2	0.7±0.7	43.6±2.5	0.07	0.56
	15	1990–2001	0.9±0.8	1.6±1.4	0	18.7±2.0	0.04	0.52

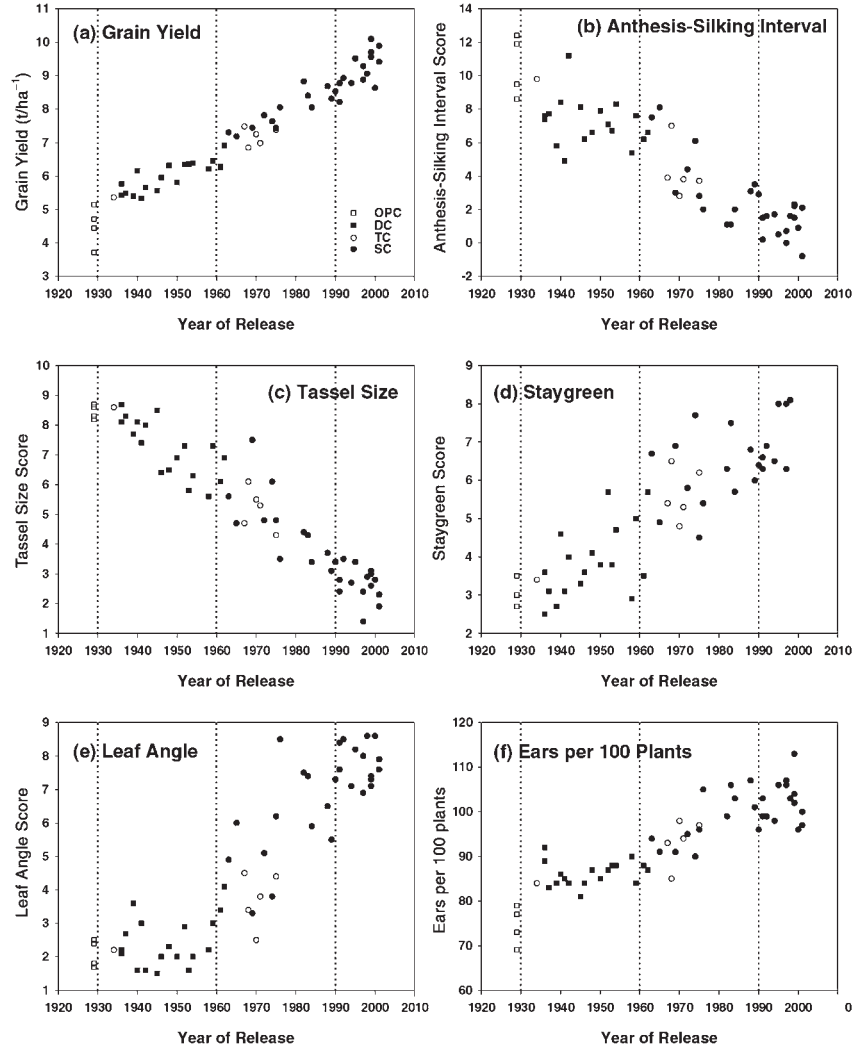


Fig. 4.5. Best Linear Unbiased Predictions (BLUPs) for hybrid grain yield and agronomic traits computed from results of Era experiments conducted from 1991 to 2001. Dotted vertical lines indicate the distinction between three time periods: 1930 to 1959, representing the period dominated by double-cross hybrids; 1960 to 1989, representing the period when the Stiff Stalk and Non Stiff Stalk heterotic groups were developed and single-cross hybrids were introduced; and 1990 to 2001, representing the modern period dominated by single-cross hybrids. All data are BLUPs based on three plant densities: 30, 54, and 79 thousand plants/ha. Key to symbols: OPC, open pollinated cultivars; DC, double cross hybrids; TC, three-way cross hybrids; SC, single cross hybrids.

performance of older hybrids under today's growing conditions may be different than it was when they were at their peak of use and popularity. One could speculate that the older hybrids might not yield as much now as they did at the time of their widespread use, or that they may yield more. For example, in a different crop in another part of the world, an IRRI (International Rice Research Institute) rice variety (IR8) yields less today than it did when first released 30 years ago. A time-series of IRRI rice cultivars, grown today, shows linear increases in yield but the highest yielding variety of recent vintage yields no more than the old variety did at the time of its release (Peng et al. 1999).

To answer the question, How did the hybrids yield in their "era" compared with the present time?, we compared yields of Era hybrids during their "peak years" (years of widespread sales) with yields of the same hybrids in the Era trials of 1996 to 2000. Data for the peak years were taken from concurrent reports of standard small-plot performance trials grown in central Iowa. Data from the present-day Era trials were for yield at the optimum plant density (the plant density with the highest yield) of each hybrid. Fig. 4.6 shows that yields of hybrids in their

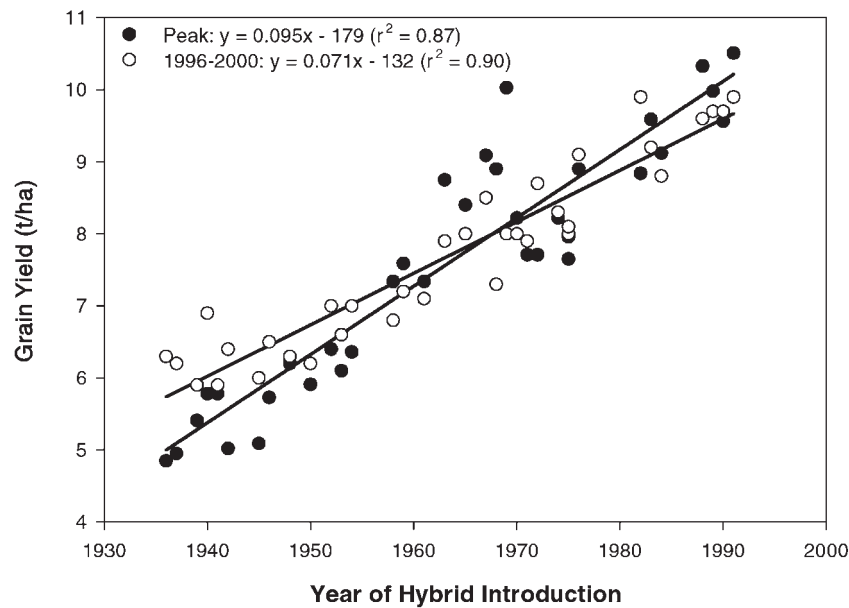


Fig. 4.6. Yields of Era hybrids in 1996 to 2000 Era trials and in their "peak" years (years of widespread planting). Yield data for "peak" years are from contemporary reports of Pioneer hybrid performance trials in central Iowa. Data for Era trials are for optimum plant density for each hybrid.

peak years corresponded closely with yields in the 1996 to 2000 trials. (Comparisons were for 36 hybrids introduced from 1936 through 1991.) Yields increased linearly in both sets (“peak” and “1996 to 2000”) and the correlation between the two data sets was 0.90 (data not shown). However, the oldest hybrids tended to yield less in their peak years than in the 1996 to 2000 Era trials and conversely the newest hybrids yielded slightly more in their peak years than in the Era trials. One can speculate that the old hybrids’ yields were higher in 1996 to 2000 than they were in the 1930s and 1940s because the current trials had better weed control and/or higher levels of available nitrogen, but this cannot be proven. And one could speculate that the weather was more conducive to high yields in the late 1980s and early 1990s (when the new hybrids were at their peak years) than it was in the late 1990s. But even if these speculations were true, undoubtedly there were several other differences, abiotic and biotic, that cannot be determined today with any degree of certainty. And at any rate the loss/gain in yield between peak year and Era yields (as indicated by regression lines) is small. The main conclusion that can be drawn from this comparison is that yields of the older hybrids have not been underestimated and yields of the newer hybrids have not been overestimated in the recent Era trials.

2. Heterosis: Single-crosses vs. Parental Inbreds. The genetic gains in yield of the Era hybrids conceivably can be caused (1) by increases in heterosis, and/or (2) by improvements in non-heterotic components of the genome, such as in those traits governed primarily by additive gene action. To test the relative importance of heterosis, comparisons were made between pairs of inbreds representing the most widely used male and female inbreds of each decade and the single-crosses of those inbreds. Within each decade (1930s through 1980s), seven pair-wise comparisons were set up as follows: an inbred from the female side of an Era hybrid was crossed with an inbred from the male side of the same hybrid, to maximize potential heterosis. Inbreds and their single-crosses (a total of 42 single-crosses) were compared in split-plot yield trials. Heterosis was calculated as $SX - MP$, the difference between the yield of the single-cross (SX) and the mean yield of its inbred parents (MP, “midparent mean”).

The results of this experiment (as well as of an earlier experiment of similar design) indicate that on the average, hybrid yield gains over the decades (1930s to 1980s) owe very little to increases in heterosis (Duvick 1984, 1999). The linear increase in single-cross yield over the decades is closely paralleled by linear increases in yield of the inbred parents of those single-crosses and consequently $SX - MP$ is constant over the decades on average (Fig. 4.7). And if heterosis ($SX - MP$) is calculated

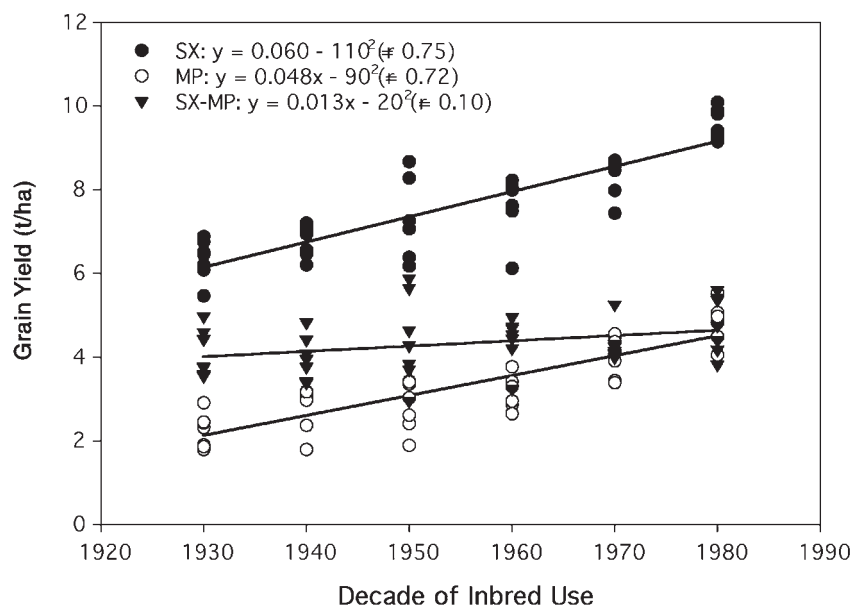


Fig. 4.7. Yields of single crosses (SX) and their inbred parent means (MP), and heterosis as $SX - MP$. Single-cross pedigrees are based on heterotic inbred combinations in the Era hybrids during the six decades, 1930s through 1980s, 12 inbreds and six single crosses per decade. Means of trials grown in three locations in 1992 and two locations in 1993 at three densities (30, 54, and 79 thousand plants/ha) with one replication per density.

as percent of mid-parent yield, the value for heterosis actually declines in linear fashion across the decades ($b = -1.7\% \text{ yr}^{-1}$, $R^2 = 0.33$ for means of 1992–93 at 30, 54, and 79 thousand plants/ha). The reason, of course, is that a constant value for heterosis is divided by increasingly large values for mid-parent yield.

However, the data on hand do show that over the decades heterosis has increased to a greater extent in trials subjected to severe stress than in trials grown in high-yield (lower stress) environments. Examples of stressful environments would be dense planting (e.g., 79 thousand plants/ha) or the abnormally cold wet season of 1993 (Fig. 4.8). This interaction of heterosis with environmental stress simply restates the fact that during the past 70 years of breeding and selection, yielding ability under stress has been improved to a greater extent in hybrids than in their inbred parents.

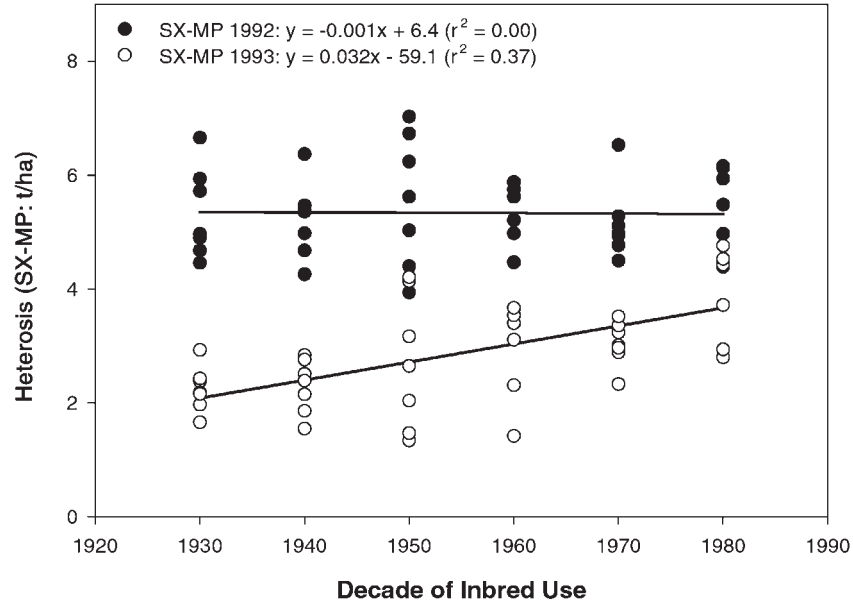


Fig. 4.8. Heterosis (as SX – MP) in two seasons, 1992 and 1993. Single-cross pedigrees based on heterotic inbred combinations in the Era hybrids during the six decades, 1930s through 1980s, 12 inbreds and six single crosses per decade. Trials were grown in three locations in 1992 and two locations in 1993. Means of three densities (30, 54, and 79 thousand plants/ha) with one replication per density.

Heterosis can be calculated on the basis of yield at optimum plant density of single-crosses and of each of their inbred parents. As stated earlier, yield at optimum plant density seems best for comparing hybrids of different eras—each hybrid is evaluated at an approximation of the plant density at which it had been bred and tested. The same argument could be used for comparing inbred lines and their single-crosses. Additionally, one could hypothesize that inbreds on average will require higher plant densities than single-crosses for maximum yield because the inbreds are smaller and will require more plants per acre to produce an equivalent leaf area index (LAI).

Analysis of the 1992–93 data for yield did not bear out this hypothesis. The inbreds interacted with plant densities in about the same manner as the single-crosses. The only obvious difference was that although the oldest single-crosses (of the 1930s and 1940s) lost yield (on average)

at 79 thousand plants/ha as compared with their performance at 30 and 54 thousand plants/ha, the inbreds from those early decades did not show a yield reduction at 79 thousand plants/ha. They maintained (but did not gain) yield at the 79 thousand plants/ha density. Both categories (inbreds and single-crosses) showed an increasing adaptation to high plant densities, progressing from earliest to most recent decades; that is, their yield at the higher plant densities was increasingly greater than that at the lower plant densities.

When heterosis calculations are based on yield at optimum plant density, the net result is that trends and values for heterosis are very similar to those determined on the basis of 3-density means. Inbred yields and single-cross yields at optimum plant density increase in linear fashion, and in equivalent amounts, over the decades. Heterosis calculated as $SX - MP$ shows no significant change over the decades. And when heterosis (as $SX - MP$) is calculated as percent of mid-parent yield, the value for heterosis declines in linear fashion across the decades ($b = -1.8\% \text{ yr}^{-1}$, $R^2 = 0.38$ for 1992–93 means). These values for optimum plant density are almost identical to results of similar calculations for the 3-density means.

B. Pedigree Examination

Study of the Era hybrid pedigrees can identify the germplasm sources (founder sources) of hybrids in the time-series. It also can reveal the continuity or extinction of breeding families that trace back to those founders. And finally it can show the breadth (or narrowness) of the germplasm base that has supported Era hybrids during any particular time, such as the decade of the 1950s or the decade of the 1990s.

1. Founder Sources. The time-series of Era hybrids through the year 2000 traces back to 53 founder sources (Duvick et al. 2003) (Table 4.4). Landraces predominate in this list, and they come primarily, but not entirely, from the U.S. Corn Belt—they are “Corn Belt Dents.” However, founders also came from the southeastern and eastern United States, and (rarely) from Latin American countries such as Argentina. Synthetic populations and first generation inbred lines also are identified as founder sources; all of these are essentially U.S. Corn Belt Dent in breeding.

2. Proportionate Contribution of Founders. The above count of the number of founder genotypes gives an indication of the potential amount of genetic diversity that could have contributed to genomes of the Era hybrids. But it is also important to know which family lineages have

Table 4.4. Founder inbred lines and open pollinated cultivars (OPC) of hybrids in Table 4.1. Source: Duvick et al. 2003.

Founder germplasm ^z	Background	OPC Background	Origin	Country
A237	Minnesota 13 × Reid Yellow Dent Population	Minnesota 13 & Reid	Minnesota	USA
ABCOMP	Pioneer Composite A × Pioneer Composite B		Iowa	USA
AFLF	Argentinean Flint/Lady- finger Popcorn	Argentinean Flint & Ladyfinger popcorn		Argentina/ USA
ALBRTFLINT	Alberta Flint Population	Alberta Flint	Alberta	Canada
ARGMAIZARM	Argentinean Maiz Amargo	Argentinean Maiz Amargo		Argentina
BH940				USA
BLACKSDCO	Black's County Reid Dent; landrace selection from Reid	Blacks (Reid)		USA
BLF				USA
BOONECOWH	Boone County White	Boone County White		USA
Luxe's Boone County White White Mastodon		Luxe's Boone County White Mastodon		USA
BR2USDA				USA
BROOKINGS86	Developed from Minnesota 13	Minnesota 13		USA
BSSS	Iowa Stiff Stalk Synthetic			USA
I 461-73 Troyer Reid		Reid		USA
AH 83 Funk 176A Reid		Reid		USA
TR9-1-1-6 Troyer Reid		Reid		USA
F1B1-7-1 Troyer Reid		Reid		USA
CI 540 Illinois Two Ear		Leaming		USA
Hy Illinois High Yield		Hy		USA
CI 187-2 Krug		Krug		USA

(continued)

Table 4.4. (Continued)

Founder germplasm ^z	Background	OPC Background	Origin	Country
BSSS (<i>cont.</i>)				
LE23 Illinois Long Ear (Leaming)		Leaming		USA
Ill 2E Illinois Two Ear (Leaming)		Leaming		USA
CI 617 Funk 176A Reid		Reid		USA
A3G-3-1-3 I159		Iodent (Reid) &		USA
(Iodent Reid) × BL345		Blacks (Reid)		
(Black's Reid Yellow Dent)				
Iodent Reid		Iodent (Reid)		USA
I 224 Iodent Reid		Iodent (Reid)		USA
OS 420 Osterland		Osterland (Reid)		USA
(Selection From Reid)				
WD 456 Walden Dent		Walden (Reid)		USA
(Selection From Reid)				
OH 3167B Clarage		Clarage		USA
COKER616		Coker Synthetic	Southern US	USA
DOCKDRF 101	Dockendorf 101 Synthetic		Iowa	USA
FCOMP2	Pioneer Female Composite			USA
FSOUTH ^y	Pioneer Far South Open Pollinated	Southern US OPCs		USA
FUNKS176A	Funks 176A; population selected from Reid	Reid	Illinois	USA
FUNKYDENT	Funks 176A; population selected from Reid	Reid	Illinois	USA
G16Y	Inbred from Lancaster Sure Crop landrace	Lancaster Sure Crop	Iowa	USA
GE440	Inbred line HT resistance source		Georgia	USA

GOLDENGATE					
ILLHY	Illinois High Yield-inbred from Hy population	Goldengate	Illinois	USA	
ILLOEAR	Illinois Low Ear population			USA	
ILLONG	Illinois Long Ear; Leaming open-pollinated cultivar		Illinois	USA	
ILLTWOEAR	Illinois Two Ear; Leaming open-pollinated cultivar	Leaming		USA	
IODENT	Iodent Selection from Reid	Iodent (Reid)	Iowa	USA	
K140	Inbred line		Iowa	USA	
KRUG	Krug-Reid and Goldmine	Krug	Iowa/Illinois	USA	
LADYFINGER	Ladyfinger Popcorn	Ladyfinger popcorn		USA	
LAGUNAOP	Laguna open-pollinated- developed by USDA from Laguna Population	Laguna population		Mexico	
LANCCOMP	Lancaster Composite-from Lancaster Sure Crop landrace	Lancaster Sure Crop		USA	
LANCLOBRK	Lancaster Low Breakage- population from Lancaster Sure Crop landrace	Lancaster Sure Crop		USA	
LANCSURCROP	Lancaster Sure Crop-Open- pollinated landrace cultivar	Lancaster Sure Crop		USA	
LE	Illinois Long Ear developed by Pioneer	Leaming	Iowa/Illinois	USA	
LLE	Lindstrom Long Ear	Lindstrom		USA	
LONGFELT	Longfellow open-pollinated landrace cultivar	Longfellow	Kansas	USA	
M3204	Mississippi 3204 hybrid		Mississippi	USA	
MA111				USA	

(continued)

Table 4.4. (Continued)

Founder germplasm ^z	Background	OPC Background	Origin	Country
MARYLDYDENT	Maryland Yellow Dent	Maryland Yellow Dent		USA
MHW				USA
MIDLAND	Midland Yellow Dent	Midland	Kansas	USA
MINN13	Minnesota 13 open-pollinated cultivar	Minnesota 13	Minnesota	USA
NWDENT	Northwestern Dent; Indian cultivar or Red Flint × White Dent	Northwestern Dent		USA
OSTERYDNT	Osterland open-pollinated cultivar (selection from Reid)	Osterland (Reid)	Iowa	USA
PROLC	Prolific Composite	Reid		USA
REID	Reid Yellow Dent open-pollinated cultivar	Reid	Minnesota	USA
SPROL	Pioneer Prolific Composite		Minnesota	USA
SYNWF9	Wilson Farm Reid Synthetic	Reid		USA
TROYERREID	Troyer Reid, selection from Reid Yellow Dent	Reid		USA
U886				USA
UHTSOURCE	University source of resistance to <i>Helminthosporium turcicum</i>			
US558W	USDA hybrid			USA
WFRYD	Wilson Farm Reid Yellow Dent; landrace selection from Reid	Reid		USA

^zFounder sub-sets are in lowercase.

^ySynthetic of southern U.S. open-pollinated cultivars.

persisted over the decades, and in what proportions. Forty-two founder genotypes contributed more than 1% in any single decade (Duvick et al. 2003) (Table 4.5). Of these 42, five OPCs contributed more than 5% on average across the decades (1930s through 2000s). They were 'Reid Iodent' (15%), 'Krug' (8%), 'Lancaster Sure Crop' (6%), 'Leaming' (6%), and 'Reid Yellow Dent' (33%). An improved population, 'Iowa Stiff Stalk Synthetic' (BSSS), also contributed significantly (mean per decade of 22%). Five of the six major contributors were U.S. Corn Belt Dent in origin; the sixth contributor, 'Lancaster Sure Crop', originated in the eastern United States but it also was a dent.

3. Variability in Proportionate Contribution. The relative importance of different founder lineages has varied over time in the list of Era hybrids. Some founders have risen and then fallen in importance. For example, 'Krug' reached a peak use of 23% in the 1940s, but then rapidly declined to a steady level of about 3%. 'Lancaster Sure Crop' peaked twice, at 11% in the 1940s and 11% in the 1970s, and is currently in decline at about 3%. 'Reid Yellow Dent' was a prominent contributor in the early decades, ranging from 40 to 50% through the 1950s. It has since declined in importance but is still a significant contributor, at levels of 20 to 30% for the past five decades. 'Reid Iodent' is the only founder that was present in the first decade and has not only persisted but has increased in importance during recent decades, starting from a level of about 5% in the 1950s and moving up to its present contribution (in the 2000s) of 26%.

Some founders made initial contributions but have since disappeared. For example, 'Illinois Low Ear' was at 25% concentration in the 1930s but abruptly disappeared in the 1940s, 'Maryland Yellow Dent' contributed 5% in the 1960s and then disappeared, and 'Boone County White' appeared in the 1960s and was gone by the 1980s.

Other founders appeared late in time and have persisted since then. Argentinean Maiz Amargo appeared in the 1980s and has contributed 4% to 5% in each of the past two decades. 'Pioneer Female Composite' and 'Pioneer Prolific Composite' appeared in the 1980s and 1990s, respectively. They have contributed between 3% and 8% per decade since their first appearance.

Some founders have persisted throughout many or all of the decades but always at a low level. For example, 'BSSS-Clarage' has never exceeded 3%, 'Lindstrom Long Ear' has varied between levels of 1% to 4%, and the inbred Hy has never exceeded 5%.

Table 4.5. Percentage contribution per decade (by pedigree) for each of 42 founder genotypes that contributed more than 1 percent in any single decade. Source: Duwick et al. 2003.

Founder genotypes	Pedigree background	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s	Decade mean
LANDRACES										
Argentinean Maiz Amargo	ARGMAIZARM	0	0	0	0	0	2.5	5.38	4.36	1.53
Boone County White	BOONECOWH	0	0	2.08	1.01	0.88	0	0	0	0.5
Clarage	BSSS-CLARAGE	0	0	0	1.33	2.48	2.38	2.46	2.21	1.36
Krug	BSSS-KRUG	0	0	0	1.33	2.48	2.38	2.46	2.21	1.36
Krug	KRUG	10	22.92	12.5	3.13	1.34	0.63	0.98	0.5	6.5
Krug Total		10	22.92	12.5	4.46	3.82	3.01	3.44	2.71	7.86
Lancaster Sure Crop	LANCCOMP	0	0	0	1.79	7.81	0.94	1.97	1.89	1.8
Lancaster Sure Crop	LANCLOBRK	0	0	0	0	2.68	2.51	2.34	1.56	1.14
Lancaster Sure Crop	LANCSURCROP	5	11.46	7.81	0.34	0.29	0	0	0	3.11
Lancaster Total		5	11.46	7.81	2.13	10.78	3.45	4.31	3.45	6.05
Leaming	BSSS-LEAMING	0	0	0	3.98	7.45	7.15	7.38	6.63	4.13
Leaming	ILLONG	0	0	0	0	0.11	1.88	1.46	0.99	0.55
Leaming	ILLTWOEAR	5	0	0	0	0.11	1.88	1.46	0.99	1.18
Leaming Total		5	0	0	3.98	7.67	10.91	10.3	8.61	5.81
Lindstrom Long Ear	LLE	0	0	1.04	5.14	4.09	2.3	1.94	3.61	2.27
Maryland Yellow Dent	MARYLDYDENT	0	0	0	3.57	0	0	0	0	0.45
Midland	MIDLAND	0	0.26	12.5	15.18	0.78	5.01	3.24	2.55	4.94
Minnesota 13	BROOKINGS86	0	0	0	0	0	1.26	0.68	0.34	0.29
Minnesota 13	MINN13	0	0	3.25	5.36	3.89	5.53	3.63	6.2	3.48
Minnesota 13 Total		0	0	3.25	5.36	3.89	6.79	4.31	6.54	3.77
Reid Yellow Dent	BSSS-Blacks	0	0	0	0.64	1.19	1.14	1.18	1.06	0.65
Reid Yellow Dent	BSSS-Butler	0	0	0	0.64	1.19	1.14	1.18	1.06	0.65
Reid Yellow Dent	BSSS-Funks	0	0	0	2.65	4.97	4.77	4.92	4.42	2.72
Reid Yellow Dent	BSSS-Osterland	0	0	0	1.33	2.48	2.38	2.46	2.21	1.36

(continued)

Reid Yellow Dent	0	0	0	0.64	1.19	1.14	1.18	1.06	0.65
Reid Yellow Dent	0	0	0	2.65	4.97	4.77	4.92	4.42	2.72
Reid Yellow Dent	0	0	0	1.33	2.48	2.38	2.46	2.21	1.36
Reid Yellow Dent	0	8.33	0	0	0	0	0	0	1.04
Reid Yellow Dent	0	0	0	0.89	3.89	0.47	0.79	0.67	0.84
Reid Yellow Dent	0	10.68	16.67	3.57	0	2.68	2.6	2.29	4.81
Reid Yellow Dent	30	8.33	2.08	0	0	0.59	0.91	0	5.24
Reid Yellow Dent	10	3.65	2.22	3.97	1.02	1.68	0.65	1.61	3.1
Reid Yellow Dent	0	20.83	25	7.14	7.8	0.63	1.36	1.35	8.01
Reid Yellow Dent Total	40	51.82	45.97	25.45	31.18	23.77	24.61	22.36	33.15
Reid-Iodent	0	0	0	3.31	6.21	5.96	6.15	5.52	3.39
Reid-Iodent	10	5.21	4.95	14.13	11.2	17.14	11.73	20.48	11.86
Reid Iodent Total	10	5.21	4.95	17.44	17.41	23.1	17.88	26	15.25
Landrace Total	70	91.67	90.1	85.05	82.21	83.22	77.87	76.79	82.94
OTHER SOURCES									
Dockendorf 101 Synthetic	0	0	0	0	0	5	0	1.34	0.79
Hy	0	0	0	1.33	2.48	2.38	2.46	2.21	1.3
Hy	5	0	2.08	4.02	2.46	0	0	0	1.7
Hy Total	5	0	2.08	5.35	4.94	2.38	2.46	2.21	3
Illinois Low Ear Population	25	0	0	0	0	0	0	0	3.13
Pioneer Composites A x B	0	0	0	3.57	3.57	0	0	0	0.9
Pioneer Female Composite	0	0	0	0	0	7.5	8.8	4.54	2.61
Pioneer Prolific Composite	0	0	0	0	0	0	5.47	3.07	1.03
Inbred line	0	2.08	2.08	0	0	0	0	0	0.52
Inbred line	0	0	0	3.57	3.57	0	0	0	0.9
Mississippi hybrid	0	0	0	0	1.79	0	0	0	0.22
BSSS ^z	0	0	0	21.2	39.72	38.13	39.35	35.34	21.72

^zAlready broken out to pedigree sources.

C. Molecular Marker Changes

Although informative, pedigree data have limitations because they do not positively identify genetic materials in the pedigree lineages, either qualitatively or quantitatively. Molecular marker data can give positive identification of genetic material. For example, one can trace a given DNA fragment from one generation to the next, and thus enable quantification of the amount of founder germplasm that persists in successive generations.

1. Number of Alleles. In a previous report, we used SSRs to enable such quantification and identification of genetic materials, scoring 969 alleles for the 1930 to 2000 array of Era hybrids and OPCs (Duvick et al. 2003). These alleles were identified from a study of 100 SSR loci distributed across all 10 chromosomes. Table 4.6 shows numbers, frequencies, and percent change from the previous decade for these SSR alleles. It shows that the number of alleles fluctuated from decade to decade, that about 40% to 50% of the 968 alleles were present in any one decade, and that there is a weak trend toward fewer numbers per decade, starting in the 1980s.

2. “New” Alleles. “New” SSR alleles in the context of this report are defined as those that have not been identified in any previous decade. Table 4.7 enumerates new SSR alleles, as found in the array presented in Table 4.6. The figures for hybrids of the 1930s may be inflated because of the small sample of OPCs to which they were compared. The large increase in “new” alleles from the 1930s to the 1940s agrees with

Table 4.6. Number of SSR alleles in each decade, percent change from previous decade, and percent of total identified in the hybrid series through 2000. Source: Duvick et al. 2003.

Decade	No. of alleles	Change from previous decade	% of total found in study (968)
1920s	387		40%
1930s	480	+24%	50%
1940s	590	+23%	61%
1950s	484	-18%	50%
1960s	599	+24%	62%
1970s	543	-9%	56%
1980s	430	-21%	44%
1990s	476	+11%	49%
2000s	369	-22%	38%

Table 4.7. Number of “new” alleles in hybrids released during each decade. Source: Duvick et al. 2003.

Analyses		No. “new alleles”							
		1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s
No. “new” alleles		241	105	44	48	30	29	19	26
No. loci with “new” alleles		84	61	36	39	24	24	15	20
No. chromosomes with “new” alleles		10	10	10	10	10	9	8	8
“New” alleles per inbred	min	17	0	0	0	0	0	0	0
	max	43	19	21	13	11	9	6	6
	mean	26.7	9.6	3.6	2.9	3.2	4.6	2.2	1.9
“New” alleles per hybrid	min	82	15	1	4	0	7	1	2
	max	121	53	30	22	16	13	7	10
	mean	97.6	38.2	15.3	9	7	9	3.6	3.9

the pedigree data, which showed that several founder families were dropped, and others were introduced, in the 1940s.

The several categories of examination (loci with “new” alleles, “new” alleles per inbred, etc.) generally agree in showing a reduction in “new” alleles starting in about the 1960s or 1970s. This corresponds with the time during which Era hybrids shifted from double-cross to single-cross status (with an intermediate stage in which some hybrids were 3-way crosses or “modified” single-crosses, meaning one parent was a cross of closely related inbreds).

3. Formation of Stiff Stalk and Non Stiff Stalk Heterotic Groups. Recent work has expanded the number of SSR loci, from 100 to 298, measured on the parents of the Era hybrids. The number of OPCs was increased from 3 to 8. Germplasm from ‘Lancaster Sure Crop’, ‘Leaming’, ‘Minnesota 13’, and ‘Midland Yellow Dent’ is now represented, in addition to that from ‘Reid Yellow Dent’ and ‘Krug’. The average number of alleles per locus was estimated for the OPCs and the hybrids and their female and male parents by decade (Fig. 4.9). The average number of alleles per locus decreased over time. There was a decrease from the OPCs to the double-cross hybrids (1930s to 1960s) and a further decrease with the move from double-cross hybrids to single-cross hybrids (1970s to 2000s). However, several of the OPCs that feature in the pedigree backgrounds of the Era hybrids are exotic and were never grown as such in the central U.S. Corn Belt. Therefore, our measurement of the decline in

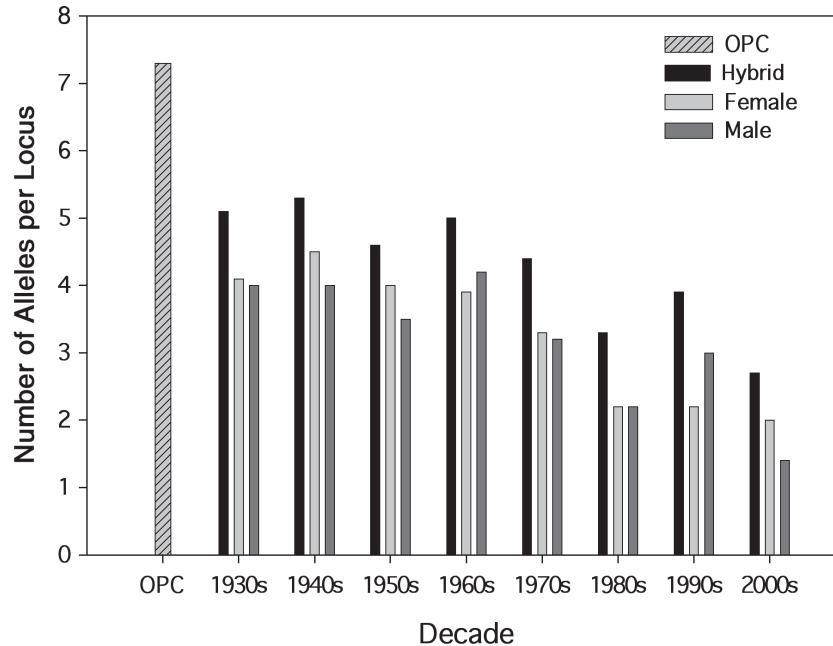


Fig. 4.9. Average number of SSR alleles per locus for 298 SSR loci for eight open pollinated cultivars (OPC) and for the Era hybrids and female and male parents of the hybrids by decade of release.

number of alleles during the transition from OPCs to hybrids may overestimate the actual decline in allelic diversity that occurred when U.S. Corn Belt OPCs were replaced by hybrids. On the other hand, our representation of OPC diversity in the central U.S. Corn Belt is more likely an underestimate of the allelic diversity that was extant in the many variations of Reid Yellow Dent and other OPCs in the central U.S. Corn Belt. More thorough surveys of OPC diversity in the 1920s are necessary to give an accurate estimate of the change in genetic diversity as OPCs were replaced by hybrids. Our intent here is to provide simply a first appraisal of OPC diversity in the 1920s and 1930s.

The number of alleles per locus was similar for the female and male parents of the hybrids in all decades. Further analysis of the allele polymorphism among the inbred parents of the Era hybrids by multidimensional scaling (Kruskal and Wish 1978) separates the older inbred parents of the double-cross hybrids from the modern inbred lines that comprise the Stiff Stalk and Non Stiff Stalk heterotic groups (Fig. 4.10). The SSR polymorphism data indicate a trend toward reduction in the

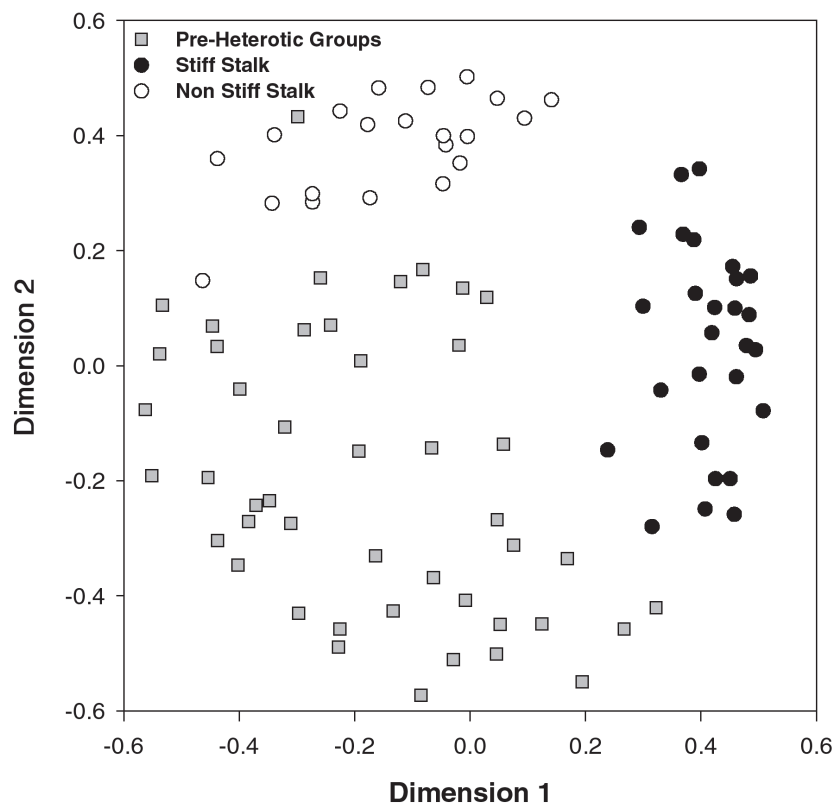


Fig. 4.10. Scores for 94 inbreds contributing to the Era hybrids on the first two dimensions of the multi-dimensional scaling analysis of the SSR polymorphism data for 298 SSR loci ($R^2 = 0.45$ for the two dimension model).

average number of alleles per locus and a clear divergence between the allele profiles of the inbreds created by pedigree breeding in the Stiff Stalk and Non Stiff Stalk heterotic groups.

III. POSTULATED CAUSES AND CONSEQUENCES OF SEQUENTIAL CHANGES IN HYBRID PERFORMANCE

A. Genetic Yield Gain

The data summarized in this review suggest that genetic yield gain primarily is caused by increase in genetic tolerance of the biotic and abiotic stresses that normally occur in a hybrid's region of adaptation.

“Yield genes” (when yield is defined as “yield per unit area”) often may simply be “stress tolerance genes,” genes that give service when needed in some seasons or some localities but not in others, depending on such factors as the weather, soil fertility, and disease pressure. This inference is based on the fact that increased yield of the Era hybrids consistently has been accompanied by increased tolerance to heat and drought, to cool and wet growing conditions, and to low- as well as high-yielding sites. This trend has lasted over a 70-year time-span. Further evidence of improved stress tolerance is the continuing improvement in standability (better root and stalk strength) and improvements in tolerance to the common disease and insect pests of the region where the hybrids are adapted.

A second way to increase yield per unit area is to improve the maize plant’s efficiency in transformation of sunlight, soil nutrients, and carbon dioxide into grain. The newer Era hybrids in this study have more upright leaves, smaller tassels, make less grain protein and more starch, and make fewer tillers. Upright leaves improve the plant’s ability to capture sunlight for photosynthesis at higher plant densities. Smaller tassels, fewer tillers and a grain protein/starch ratio changed in favor of starch presumably reduce the plant’s energy requirements for general maintenance and so make more energy available for grain production. “Efficiency genes” may be a second category of “yield genes,” differing from stress tolerance genes in that they operate at all times and all places, rather than only in particular stress conditions. But in a sense they also may be stress tolerance genes if the increased efficiency that they impart provides more energy for stressed (and presumably energy-hungry) plants.

Of course, in regard to both stress tolerance and efficiency, it may well be that the critical genetic changes primarily are in the regulatory parts of the gene, rather than in the expressed portion. Timing of gene action or threshold levels of stimulus may be more important than the gene product per se. We consider this to be an important area of research if we are to understand the basis of the genetic improvements in adaptation of maize hybrids over the course of a breeding program.

Increases in stress tolerance and in production efficiency increase the ability of the maize hybrids to tolerate ever-higher plant densities, which invariably increase the burdens of biotic and abiotic stress. Farmers have increased their planting rates over the years (since at least the 1950s), and they therefore have increased the amounts of abiotic and biotic stress on their maize plantings, exposing the weaknesses of

hybrids that may have been satisfactory at lower plant densities. Breeders, reacting to rejection of those hybrids, have developed newer hybrids with tolerance or resistance to the biotic or abiotic stresses that were the source of trouble and have planted their new-hybrid yield trials at constantly higher plant densities. Thus, the breeders continually have increased the selection pressure for tolerance to the most troublesome stresses of previous seasons, in addition to constant selection pressure for higher grain yield. Consequently, they have produced a stream of hybrids with steadily increasing amounts of stress tolerance and continually increasing efficiency in grain production, especially in high-density plantings. They have produced hybrids with the ability to make respectable amounts of grain on every plant at ever higher plant densities and under a variety of growing conditions, both favorable and unfavorable. The net product has been a stream of hybrids that continuously outyield their predecessors year in and year out, in the region of their adaptation.

Conversely, the Era data show that the time-series' increase in yield per unit area is not due to increased yield potential per plant. The Era time-series showed little or no gain in yield at 10 thousand plants/ha (i.e., one plant per square meter). At 10 thousand plants/ha, especially in favorable seasons, individual plants presumably are nearly stress-free and can express their full yield potential. Although grain yields of individual plants of the newest hybrids averaged about 0.4 kg/plant at 10 thousand plants/ha, the newest hybrids produced their highest yields at 79 thousand plants/ha with averages of 0.13 kg/plant. Maximum grain yield per plant is not necessarily a predictor of high yield per unit area.

This study is not the only one to show that maize yield gains over the years owe much to (or at the least are associated with) increases in stress tolerance (Bänziger et al. 1999; Castleberry et al. 1984; Edmeades et al. 1997, 1999; Tollenaar and Wu 1999; Tollenaar et al. 1994, 2000). And other investigations find, as well, that changes in phenotype and physiology similar to those described herein for the Era hybrids often are associated with (and may be consequences of) improvements in yield and stress tolerance (Chapman and Edmeades 1999). The Era hybrid time-series results probably are not unique, but rather they may epitomize any selection program that has the goal of increasing varietal yield and dependability in a defined region of adaptation.

A final comment, a negative one, in regard to linear increases in grain yield: when stated as percent gain, the increases in yield will be smaller each year on average, because a constant value for yield gain is being

divided by an ever larger value for hybrid yield. Thus, the percent gain in grain yield (the rate of gain) is declining and has declined from the beginning of this time-series. Unfortunately, the cost per unit of yield gain has not declined, at least as reported in 1984 (Duvick 1984) and as can be inferred also from a recent report on human and financial resources devoted to plant breeding research and development in the United States (Frey 1996). The cost per unit of yield gain has risen continually in past years and it probably will continue to increase unless new efficiencies in breeding are introduced.

B. Correlated Responses or Lack Thereof

The maize plant has made several decisions “on its own” when subjected to intense selection for higher and more stable yield. Without express breeder intention and/or selection, successive hybrids have (for example) smaller tassels, more upright leaves, less grain protein, and shorter anthesis-silking interval. As noted earlier, these changes probably increase efficiency and stability in grain production, and are a consequence of selection for high and stable yield. It may be important that tassels cannot become much smaller or leaves much more upright, and, therefore, these changes will not be of much help in the future as ways to increase efficiency in grain production. Also, one would suppose that except for specialty hybrids, breeders would not wish to lower grain protein percentage any further.

Harvest index increased, but was minimal, approximately one percentage unit per decade, according to measurements made in 1985. The increase was much less than that shown for Green Revolution wheat and rice cultivars in the early years of those crops, but it was relatively constant and was still increasing in 1985. Fodder weight showed no increase in the 1985 measurements. One can infer, therefore, that yield gain of the newer hybrids depends on increased efficiency in production of grain per plant (increase in harvest index at the plant density for which the hybrids were bred) added to the hybrids’ generally increased tolerance to the stresses of higher density planting. Tolerance to higher density planting probably is more important than increased harvest index per se, but the probability of complex interactions between the two traits precludes any definitive statement about which is more important. Also, the harvest index data at hand are for one year only and do not include Era hybrids of recent years, so one should not attempt to infer or predict too much from them. At most, one can say that improved harvest index has played a much smaller role in yield gain of the Era maize

hybrids than it did for the early generations of the Green Revolution wheat and rice cultivars.

If protein percentage was reduced (and starch percentage increased) because more energy is needed to make protein than to make starch, one might expect oil percentage to have been reduced as well and to a greater extent, because even more energy is required for synthesis of oil. Since oil percentage was not reduced, it seems likely that a minimum grain oil percentage is required for some function, such as germination. One can hypothesize that the kernel cannot go below that limit and still function properly as (for example) a germinating seed.

Similarly, one might logically expect that if ECB2 (European corn borer, 2nd generation) tolerance/resistance is increased, ECB1 (European corn borer, 1st generation) tolerance should be increased simultaneously. The fact that it was not would seem to indicate that the factor that imparted increased tolerance/resistance to ECB2 is not present at the time of ECB1 establishment, or it is not present in tissues that ECB1 borers attack. Denser stalks or stalks with more lignin (and more resistance to stalk lodging) may be a reason for increased resistance to damage from ECB2. Such structures are not yet present during the time that ECB1 borers are active.

C. Heterosis

The minor role for heterosis in yield increase of the Era hybrids seems to be at variance with reports that show a major increase of heterosis over the years in inbred/hybrid comparisons (e.g., Meghi et al. 1984) and in population improvement programs (e.g., Carena and Hallauer 2001). This result also is at variance with the generally accepted belief that because heterosis is the basis for superiority of hybrids over their parents, further increase in yield will depend primarily on further increases in heterosis.

It is true that heterosis (as $SX - MP$) has made some increase over the decades when measured in stressful environments (Fig. 4.8), but nevertheless the data on hand indicate that heterosis for grain yield was less important than non-heterotic factors for improving yields over the years. Indeed, when heterosis (as $SX - MP$) is stated as percent of midparent yield (a frequent procedure) rather than as an absolute amount, the value for heterosis actually declines in low-stress conditions and at best is merely constant in high-stress growing conditions.

On sum, it seems likely that the primary reason for increase in yields of the Era hybrids is as summarized by Hallauer (1999, p. 486) for results

of recurrent selection. He says, “the additive effects of alleles with partial to complete dominance were of greater importance but dominant and epistatic effects could not be discounted.” A predominant but not exclusive role for additive gene action would explain the concomitant increase in yields of inbreds and their hybrids but with slightly higher average increase for hybrids than for inbreds, at least in stressful growing conditions. Again, results in this data series are not unique; other researchers have found that heterosis for grain yield and for accompanying traits such as biomass is increased in stressed environments (e.g., Giauffret et al. 1997; Meghi et al. 1984).

Finally, heterosis values for plant height or for flowering date (anthesis) have not increased at all over the years (Table 4.2). Heterosis for plant height actually has diminished, although not very consistently or to any large degree.

D. Pedigree Dynamics

The pedigree data in this study show that it is a fallacy to believe that most U.S. maize hybrids are founded upon a genetic base of only a handful of widely used public inbred lines. (The inbred lines B14, B37, B73, Mo17, and Oh43 occasionally are cited as encompassing most of U.S. maize diversity.) Indeed, one could argue from the history of migration of maize into the North American continent and its subsequent usage that this region represents a center of diversity for maize. The relative breadth of current diversity in U.S. elite maize is shown by the large number of founder lines and landraces that underpin the germplasm developed by one breeding organization for one region of the United States. The germplasm in this study includes contributions from ancestral lines originally bred in regions exotic to the central U.S. Corn Belt, (e.g., Georgia, Pennsylvania, and Tennessee). But this array does not represent the full range of diversity that currently exists in regions of the United States outside of the central U.S. Corn Belt.

The history of maize in North America does not fit the model for small grain cereals [wheat (*Triticum* spp. L.), oats (*Avena sativa* L.), barley (*Hordeum vulgare* L.), rice, millet (*Pennisetum glaucum* R. Br.), or sorghum (*Sorghum bicolor* (L.) Moench)] where relatively few inbred cultivars were brought to the United States during the past two to three hundred years. A broader diversity of maize has been extant in North America during the past two to three hundred years. Two races that are genetically very distinct (the Northern Flints and Southern Dents) were hybridized during the mid-nineteenth century to create the Corn Belt

Dents. Further crossing and selection for adaptation then was practiced by generations of farmer breeders to create the founder germplasm from which inbred lines and hybrids were initially developed in the early decades of the twentieth century. Formal breeding programs have allowed new diversity to be created by bringing together germplasms that otherwise would have been isolated in different regions of the country. Breeders therefore have continued to create and to test new combinations of diversity, a reality that differs from another misconception whereby breeders are said to have taken an initial small sample of corn inbreds and essentially then boiled away most of the diversity.

This study shows that the creation, testing, and incorporation of new diversity has accompanied the development of robust new hybrids that increasingly are tolerant of pests and stressful climatic conditions and that, consequently, can yield more per unit area of land. These increasingly robust hybrids make more effective use of available soil, water, sunlight, and nutrient resources. It seems likely that infusions of new germplasm have played an essential role in development of the improved hybrids. If this is true, we can assume that additional, fresh genetic diversity will be required to provide the potential for further adapting corn hybrids to future changes in husbandry, different climates, new forms of pests and diseases, and to new demands from consumers. An important challenge therefore will be to further increase breeders' abilities to identify and incorporate potentially useful new exotic diversity, including that from germplasm that currently resides outside the United States. Maize productivity thereby will become yet more efficient and will contribute increasingly to food, health, and environmental wellbeing.

Pedigree breeding, augmented with population improvement to create some important publicly bred Stiff Stalk lines, has been the major breeding strategy underpinning the hybrids reported upon in this study. The program has evolved into a large reciprocal recurrent selection program, with pedigree breeding operating within each of the two main heterotic groups. There has been a reduction in the average number of alleles per locus, as measured by SSRs distributed across the genome. While there has been a reduction in the number of alleles per locus within the heterotic groups, there has been a concomitant increase in diversity of alleles between the heterotic groups. The resulting pattern of change in allele diversity over time at a locus varies across positions in the genome. These changes in allele numbers per locus and in allelic diversity at individual loci may be, in part, a consequence of the combined effects of selection for favorable additive alleles within the

heterotic groups and selection for complementary alleles between the heterotic groups.

IV. SUMMARY, COMMENTS, AND PREDICTIONS

An array of commercial hybrids representing seven decades of breeding for the West-central U.S. Corn Belt shows linear increases in grain yield and in tolerance to biotic and abiotic stress, in particular to stresses typical of the West-central U.S. Corn Belt. Phenotypic changes (or lack thereof) in the hybrids partly are the result of breeders' planned selection practices and partly appear to be correlated responses to overt selection for other traits.

Increases in yield per unit area primarily are dependent on the ability of new hybrids to tolerate increased plant densities and the stresses they induce, rather than to increases in yield potential per plant, or to improvements in harvest index (when hybrids are planted at their appropriate plant density). As plant densities have increased across the years, newer generations of hybrids bred for those higher plant densities continue to make about the same amount of grain per plant at the higher plant densities, thus increasing yield per unit area.

Increases in heterosis have made a minimal contribution to the yield gains, although the contribution of heterosis in absolute amounts (calculated as $SX - MP$) increases when hybrids are subjected to increased levels of abiotic stress.

Pedigree and molecular marker analyses have shown the dynamic nature of germplasm shifts over the decades. Pedigree breeding, albeit with a few important inputs from population improvement, has been the primary breeding method during the 70 years of this long-term selection program.

Founder sources are numerous but are almost entirely of U.S. origin, especially from the U.S. Corn Belt. Over the decades, founders have appeared, disappeared, or persisted in hybrid pedigrees, as multigenerational inbred families arose, died out, or persisted. Persistent founders have varied considerably in proportionate contribution over the decades, increasing, decreasing, or sometimes maintaining a fairly constant contribution.

Molecular marker analysis of the Era hybrids and their inbred parents has shown that over the years the average number of alleles per locus has declined, and that, in recent decades, the alleles have been sorted into two contrasting groups corresponding to Stiff Stalk and Non Stiff

Stalk breeding pools. One can hypothesize that the contrasting marker alleles are associated with specific additive and/or partially dominant genes that allow inbreds in the two pools to complement each other's weaknesses. As well, they could be associated with genes affecting traits needed to make a good seed parent (Stiff Stalk) or a good pollinator parent (Non Stiff Stalk).

There is as yet no indication that yield gains are leveling out in this long-term breeding program. However, it would appear that contributions from some of the yield-enhancing trait changes (such as smaller tassels, more upright leaves, or reduced grain protein percent) have gone as far as they can go. Parenthetically, we note (and emphasize) that many of the trends that have been described in this report can be discerned as significant only because of the long-term nature of the breeding and selection program. Heritability estimates are much more robust for the 70-year period than for intervals within that period.

Past genetic gains in yielding ability have been closely associated with and dependent upon interactions with changes in agronomic practices (such as earlier planting and higher plant densities). One can expect that new and presently unforeseen changes in agronomic practices (and probably in climate) will give tomorrow's breeders new challenges and new opportunities to breed and select for enhanced yielding ability under new growing conditions and (probably) with new infusions of germplasm from around the world. Regardless of the nature of the future genetic changes, one can be confident that they will improve hybrid yields and dependability (an important aspect of yield) only if they improve the hybrids' tolerance to the prevalent biotic and abiotic stresses of future eras.

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