Chapter 2

Genetic Contributions to Yield Gains of U.S. Hybrid Maize, 1930 to 1980

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ABSTRACT

The increase in yield in commercial maize (*Zea mays* L.) hybrids attributable to genetic improvement averaged 92 kg ha^{-1} year^{-1} (linear) from 1950 to 1980 as measured by trials conducted in 1978 to 1980 on a series of 47 commercial hybrids released at intervals from 1934 to 1978 and an open pollinate of 1930 vintage. The genetic gain from 1930 to 1955 was 72 kg ha^{-1} year^{-1}; the genetic gain from 1955 to 1980 was 112 kg ha^{-1} year^{-1}. The 50-year average genetic gain of 92 kg ha^{-1} year^{-1} is equal to 89% of Iowa's estimated total yield gain over 50 years of 103 kg ha^{-1} year^{-1}. A second estimate of genetic gain from 1930 to 1980, based on sets of single cross diallels, is 73 kg ha^{-1} year^{-1}, or 71% of the total yield gain. The genetic yield gains in the commercial hybrids were accompanied by large and consistent improvements in resistance to root lodging, stalk lodging, premature plant death, and barrenness. New hybrids showed the greatest advantage in yield at high plant densities and high soil fertility levels and were consistently superior to the older hybrids in low yield environments. Successive hybrid releases tended to be increasingly tolerant to feeding by second-generation European corn borer and to have a more upright leaf habit. Plant height, ear height, leaf area index, flowering date, and grain moisture at harvest were changed little through the years. Small improvements with large hybrid-to-hybrid variation occurred for resistance to northern corn leaf blight (*Helminthosporium turcicum* Pass.), to feeding of first-generation European corn borer (*Ostrinia nublalis* Hübner), and in harvest index. Newer hybrids tended to have greater stover weight per plant, heavier kernels, fewer kernels per plant, and fewer kernel rows per ear. Trials of a series of five single cross diallels, each containing ten single crosses made by intercrossing the five most widely used inbreds per decade for the five decades, 1930 through 1970, showed

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approximately the same changes over time as the commercial hybrids. Results of the diallel experiment are interpreted as evidence that general combining ability for grain yield, standability, and stress resistance have improved through the years. However, the shape and slope of the yield response curve for commercial hybrids over the years suggests that specific combining ability also may have made an important contribution to yields, especially in recent years. Tests of the five sets of inbred parents showed approximately the same kinds of changes through time as were shown for their diallel single cross progeny. Rates of improvement in yield and standability were less for the inbreds than for their single cross hybrids, but rates of improvement in resistance to barrenness were greater for inbreds than for their single cross hybrids. Midparent heterosis for grain yield increased at a linear rate of about 40 kg ha^{-1} $year^{-1}$.

Yields of maize (*Zea mays* L.) in the USA increased in fairly regular fashion from 1930 to 1980 (Fig. 2–1). It is important to know what portion of the yield gain is attributable to genetic improvements through breeding and how much is attributable to other factors such as weather, better weed control, or more fertilizer. Several estimates have been made of the genetic contribution to yield gains of maize in Iowa. Darrah (Hallauer, 1973) estimated the genetic contribution at 33%. Russell (1974) produced estimates of 79% and 63%, and Duvick (1977) estimated the genetic contribution as 57% and 60% of the total yield gain.

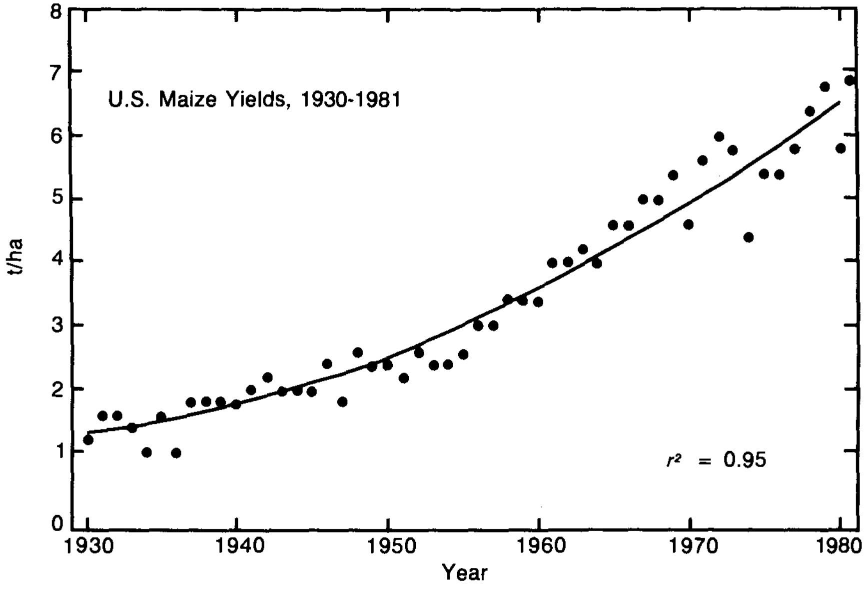

Fig. 2–1. U.S. maize grain yields from 1930 to 1981. Each point represents the mean yield for the indicated year. Regression calculated on the basis of 1930 to 1980 data using the second degree polynomial $Y = a + bX + cX^2$. r^2 = coefficient of determination. (Data obtained from various volumes of USDA's *Agricultural Statistics*, U.S. Government Printing Office, Washington, D.C.)

Darrah's estimate was based on the amount of total gain in yield of hybrids in the Iowa corn yield tests for southern Iowa during the years 1930 to 1970 compared with the gain in yield of a check hybrid. The difference between total gain (99 kg ha^{-1} $year^{-1}$) and check hybrid gain (66 kg ha^{-1} $year^{-1}$) represented the genetic component (33 kg ha^{-1} $year^{-1}$).

Russell (1974) compared hybrids representative of the period 1930 to 1970 in a single experiment. Hybrids were tested in central Iowa in the 3-year period 1971 to 1973. The yield gain associated with year of introduction, 63 kg ha^{-1} $year^{-1}$, was compared with the overall gain in average Iowa farm yields of 78 kg ha^{-1} $year^{-1}$. A second estimate adjusted the genetic gain down to 49 kg ha^{-1} $year^{-1}$ to compensate for presumed advantage because of testing sites.

Russell (1974) and Duvick (1977) both noted that the newer hybrids were improved in standability and stress resistance as well as yield potential. They also stated that high plant densities were required for maximum yield of the newer hybrids.

The three experiments described here are intended to provide additional data for making estimates of the genetic component of yield gains. They include a more complete and representative set of commercial hybrids and inbred lines than those in my earlier experiments (Duvick, 1977), carry the time scale up to about 1980, examine changes in several additional traits, and document the performance of the inbred lines used in the diallel single cross sets.

MATERIALS AND METHODS

Experiment 1

Forty-seven hybrids commercially important in central Iowa at successive intervals from 1934 to 1978 were reproduced by hand pollination at one location using inbred seed that had been preserved in cold storage (Table 2–1). An additional entry was a selection of Reid's yellow dent grown annually on a farm (the Reid farm) in central Iowa since the early 1900s and collected in the early 1960s. The 48 entries were tested in yield trials in central Iowa at two locations in 1978, three in 1979, and four in 1980. All trials were grown at three plant densities (30 000, 47 000, and 64 000 plants/ha) with one replication per density. The lowest density was typical for central Iowa in the 1930s, the middle density was typical of the 1970s, and the highest density was higher than was recommended for the 1970s. Plots were overplanted and thinned to stand. Plots consisted of two rows 631 cm long and 76 cm wide. Scores and counts were taken for several agronomically important traits. All scores were taken on a 1 to 9 basis, with 9 indicating the most favorable condition. For leaf angle, 9 indicated the most upright leaves. All trials were harvested with a combine adapted for small plots. In addition to the yield trials, special plantings, usually of three replications in one location, were innoculated with northern corn leaf blight (*Helminthosporium turcicum* Pass.), infested with European corn borer (*Ostrinia nubilalis* Hübner), or harvested as

Table 2–1. Hybrids tested in experiment 1.

Hybrid	Year of release	Hybrid	Year of release
Early cultivar†	1930	3291	1961
351	1934	3618	1961
307	1936	3206	1962
322	1936	3280	1962
317	1937	3306	1963
330	1939	3418	1963
300	1940	3376	1965
336	1940	3567	1965
340	1941	3369A	1966
339	1942	3582	1966
341	1942	3390	1967
343	1944	3571	1968
344	1945	3334	1969
335	1946	3388	1970
352	1946	3517	1971
350B	1948	3366	1972
325	1950	3535	1973
347	1950	3301A	1974
301B	1952	3529	1975
354	1953	3541	1975
329	1954	3183	1975
317A	1955	3382	1976
354A	1958	3360	1976
328	1959	3536	1978

† An open-pollinated cultivar, Neil's Reid, typical of those planted in the 1930s.

whole plants to provide data on plant and ear traits.[2] A few of the hybrids included in Experiment 1 also were compared at three levels of N fertilization in two separate split-plot experiments. Each of these experiments was grown at five locations in the Midwest in 1979.[3]

Experiment 2

Five sets of 10 single cross hybrids were compared, one set for each of the five decades 1930 through 1970. Sets were prepared by crossing in all combinations the five most widely used unrelated inbreds in Pioneer brand hybrids for central Iowa in each of the five decades (Table 2–2). This experiment was designed to allow the study of changes in general combining ability through the years in the absence of any bias that might have been induced by the change in the 1960s from double cross to single cross hybrids.

The 50 single crosses were tested in a split split-split plot experiment for 3 years (1977 to 1979) at two locations in central Iowa, at three densities per location, and with two replications for each density. Densities

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[2] Assistance for these special trials was provided by Daniel Wilkinson, John Campbell, Ferd Dicke and Nicholas Frey of the Department of Corn Breeding, Pioneer Hi-Bred International, Inc.

[3] The fertilizer experiments were designed and conducted cooperatively by several members of the Department of Corn Breeding, Pioneer Hi-Bred International, Inc. Their efforts are acknowledged with thanks.

Table 2–2. Inbreds used in experiments 2 and 3 listed by decade of important use.

1930s	1940s	1950s	1960s	1970s
HY†	PMD‡	KR-B§	B37†	B37-A¶
LDG†	PMY‡	IDT-A§	C103-A§	B73†
KR†	KR-A§	OH43†	IDT-B¶	IDT-D#
WF9†	PS98‡	PMD-A§	PMY-A§	OH43-A#
38-11†	LX33§	WF9-A§	WF9-B¶	PH7-A#

† Public inbred lines.
‡ First cycle lines.
§ Second cycle lines.
¶ Third cycle lines.
# Fourth cycle lines.

were the whole plots, sets of diallels the subplots, and single crosses in diallels the sub-subplots. All trials were handled as described for experiment 1.

All inbreds in the set representing the first decade were public lines, and all had been developed for open-pollinated cultivars. Those for all successive decades were developed by Pioneer Hi-Bred International, Inc. except for the public inbreds OH43, B37, and B73. They were usually second, third, or fourth cycle lines developed by the pedigree method except for PMD, PMY, and PS98, which were selfed from open-pollinated cultivars, B37, selected by means of early testing from cycle 0 of Iowa Stiff Stalk Synthetic, and B73, from cycle 5 of Iowa Stiff Stalk Synthetic. Inbreds of the first four sets were the same as reported in the earlier study (Duvick, 1977). In the last set, three of the five inbreds were replacements and are thought to more accurately represent important inbreds of the 1970s.

Experiment 3

The inbreds used to make the five single cross sets in experiment 2 were tested as inbreds in yield trials designed and conducted in the same way as those for experiment 2. Experiments 2 and 3 always were grown side by side, each bordered by single crosses or inbreds as appropriate.

RESULTS

Experiment 1: Commercial Hybrids

ANALYSES OF VARIANCE

Differences among hybrids were statistically significant for all traits measured except number of kernel rows per ear and harvest index in 1981. The hybrids × environments interaction was highly significant for most of the traits measured in the nine-environment yield trials. The hybrids × densities interaction generally was statistically significant for yield and standability traits but not for plant size and maturity traits. The hybrids × densities × environments interaction was used to evaluate the significance of the two first-order interactions.

CORRELATIONS

Grain yield, root lodging, stalk lodging, stay-green score (a score for the absence of premature death in September), ears per 100 plants, and resistance to ear dropping were positively and (except for ear dropping at the high density) significantly correlated with year of hybrid release at all plant densities. Plant and ear height, flowering date, grain moisture percent, and scores for seedling vigor were not significantly correlated with year of release, although the newer hybrids showed a slight tendency to be shorter and later and to have better seedling vigor.

Scores for upright leaf habit, tolerance to first- and second-generation infestations of European corn borer, and resistance to northern corn leaf blight showed statistically significant positive correlations with year of release. Leaf area index (LAI) and its components of leaf number, leaf width, and leaf length showed no significant correlation with year of release. Leaf area index values at 47 000 plants/ha averaged 3.23 in 1979, a dry year.

Correlations of year of release with several measurements of plant and ear traits indicated that newer hybrids had heavier kernels, fewer kernel rows per ear, fewer kernels per plant, and higher stover weight. Correlations of year of hybrid release with kernels per row were not significant. Newer hybrids had a significantly higher harvest index in 1980, a year of severe drought, but not in 1981, a year with favorable weather for maize yields. The 1980 correlation of harvest index with year of hybrid release, although statistically significant, was not large ($r = 0.28$). Harvest index values at 47 000 plants/ha averaged 0.34 in 1980 and 0.47 in 1981.

Several traits improved together with yield through the years. Resistance to root and stalk lodging, ears per 100 plants, favorable stay-green scores, and high tolerance to second-generation corn borer were highly correlated with high grain yields. Late maturity was only moderately associated with high yield whether measured as flowering date or grain moisture percent, and high plant and ear height were not associated with high yields.

Several tests of degree of tolerance to second-generation infestation of European corn borer under natural and artificial infestation agreed in showing that the newer hybrids were on the average significantly more tolerant. Visual differences among hybrids in the field in 1978, a year of exceptionally heavy natural infestation, were especially striking. Many of the older hybrids were severely damaged by the borer, whereas most of the newer hybrids showed little visible evidence of borer infestation.

REGRESSIONS

The best-fit regression (quadratic) of hybrid yields on year of hybrid introduction showed yields ascending at an increasing rate over time (Fig. 2–2). The scatter graph of hybrid mean yields did not show a clear-cut shift to higher-yielding hybrids at the point double crosses were replaced by single crosses, in about 1963. However, the best-fit regression for the 29 nonsingle cross entries of 1930 to 1963 was linear. Projected to 1980, it

Table 2–3. Linear regressions of several hybrid traits on year of release, experiment 1.†

	Plants/ha			
	30 000	47 500	64 000	Mean
Character	Unit change/year			
Grain yield (kg/ha)	60	110	120	90
Percent of plants not root lodged	0.6	1.0	1.1	0.9
Percent of plants not stalk lodged	0.6	0.6	0.5	0.5
Stay-green score‡	0.1	0.1	0.1	0.1
Ears/100 plants	0.3	0.3	0.4	0.3
Percent of plants with no ears dropped	0.04	0.04	0.01	0.03

† Calculated from means of 48 hybrids at nine locations with one replication per density.
‡ Stay-green scores were taken at eight locations.

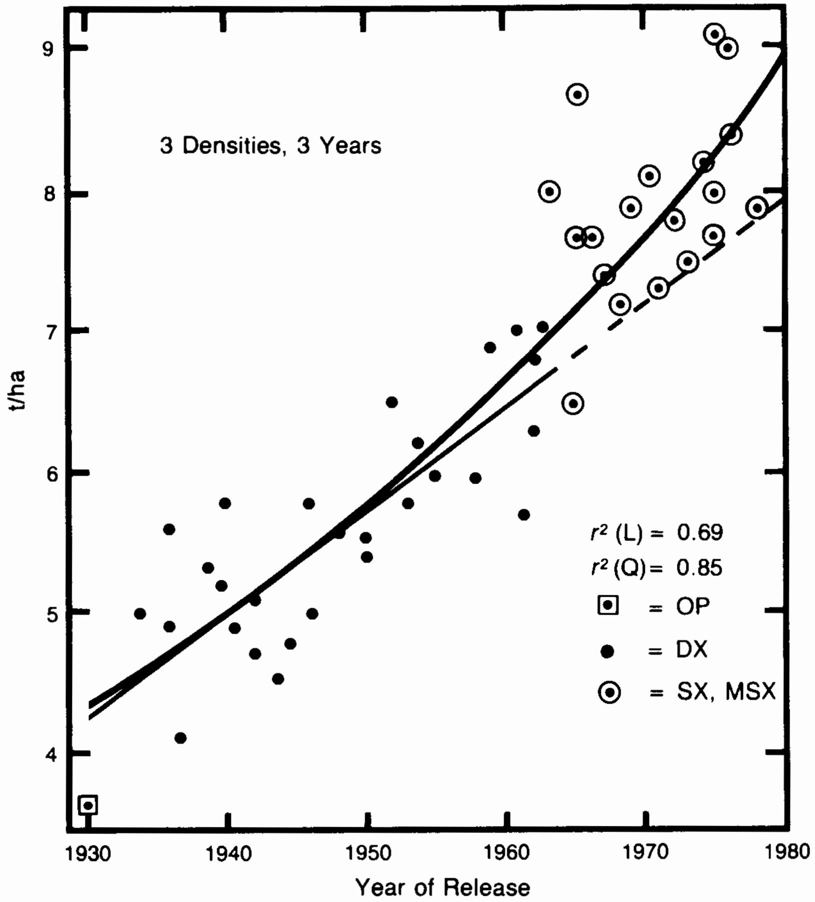

Fig. 2–2. Mean grain yields of hybrids in experiment 1. Square with enclosed dot indicates open pollinate (*OP*); solid dots indicate double cross hybrids (*DX*); circles with enclosed dot indicate single cross (*SX*) or modified single cross hybrids (*MSX*). Quadratic regression (*Q*) is based on all 48 entries (1930 to 1978); linear regression (*L*) is based on the 29 non-single cross entries (1930 to 1963). Dashed line projects linear regression to 1980. r^2 = coefficient of determination for each regression.

predicted average yields well below those actually achieved by the single cross hybrids of the period 1963 to 1978 and about 1 t/ha below the yield predicted by the curvilinear regression calculated from the complete 1930 to 1978 data set (Fig. 2–2).

Linear regressions of several traits on year of hybrid release indicate that plant densities sometimes affect calculated rates of gain (Table 2–3). Annual gains for grain yield and for percent of plants without root lodging were only half as great at the low plant density as at the high plant density. Rates of gain for stalk-lodging resistance, stay-green scores, and ears per plant were relatively unaffected by changes in plant density.

Grain yields appeared to be approaching a plateau at 30 000 plants/ha, showed a straight line increase at 47 000 plants/ha, and ascended at an increasing rate at 64 000 plants/ha (Fig. 2–3). The highest yields of the newer hybrids were at the medium and high densities. The highest yields of the older hybrids were at the low density, typical of the 1930s. From this graph, we can estimate the rate of gain in genetic yield potential from 1950 to 1980 if we assume that hybrids yielded 4.7 t/ha in 1930 (the predicted yield for 1930 at the 1930s density of 30 000 plants/ha) and 9.3 t/ha in 1980 (the predicted yield for 1980 at the 1980s density of 47 000 plants/ha). The genetic gain over 50 years (4.6 t/ha) averaged 92 kg ha^{-1} $year^{-1}$. This figure may be conservative for estimating recent rates of gain, because the data illustrated in Fig. 2–3 indicate a genetic gain of 72 kg ha^{-1} $year^{-1}$ from 1930 to 1955 but 112 kg ha^{-1} $year^{-1}$ from 1955 to 1980 using yields indicated for 30 000 plants/ha in 1930, either 30 000 or 47 000 plants/ha in 1955, and 47 000 plants/ha in 1980.

Rates of gain for percent of plants without root lodging were greatest at the medium and high densities, but even at the low density, which had the least amount of root lodging, hybrids improved steadily and in significant amounts through the years (Fig. 2–4).

Rates of gain for percent of plants without stalk lodging showed little interaction with densities (Fig. 2–5). The best fits for regression of this trait on year of introduction were curvilinear for medium and high densities but only linear at the low density.

Stay-green scores showed linear and remarkably similar rates of gain over time at all three densities (Fig. 2–6). Scores were similar in the three densities.

Newer hybrids tended to be multiple eared at 30 000 plants/ha but not at the higher densities (Fig. 2–7). Perhaps of more significance is the fact that the newer hybrids tended to be more resistant to barrenness at the higher densities.

The newer hybrids tended to have a more upright leaf habit, as indicated by higher leaf angle scores (Fig. 2–8). Resistance to northern corn leaf blight and tolerance to first-generation European corn borer, although positively and significantly correlated with year of release, showed very little gain over the 50-year period (Fig. 2–8). Low r^2 values indicated a large variation among hybrids within a given release period for these two traits. A study of individual hybrid scores showed that although some of the new hybrids were significantly superior for these traits, others were not.

Tolerance to second-generation infestation of European corn borer showed relatively large average gains over time as tested with natural or

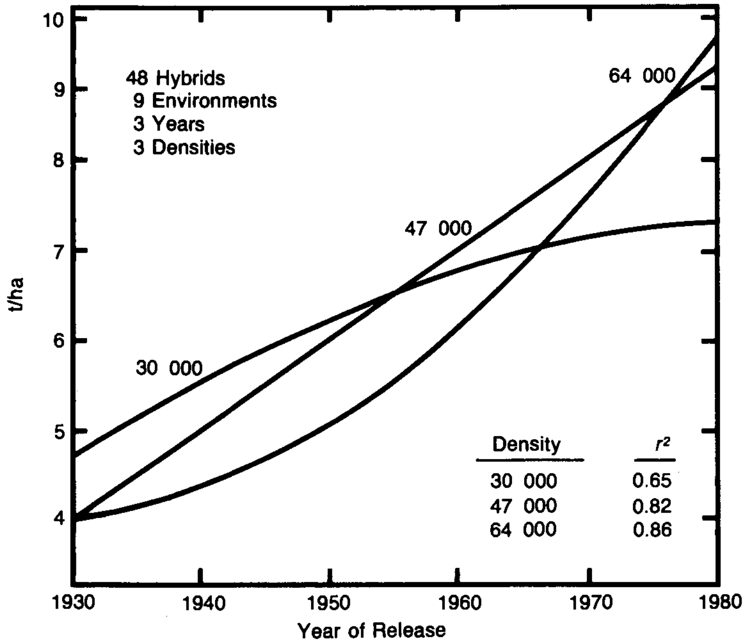

Fig. 2–3. Regressions of hybrid grain yield at each density on year of hybrid release, experiment 1. r^2 = coefficient of determination for each regression.

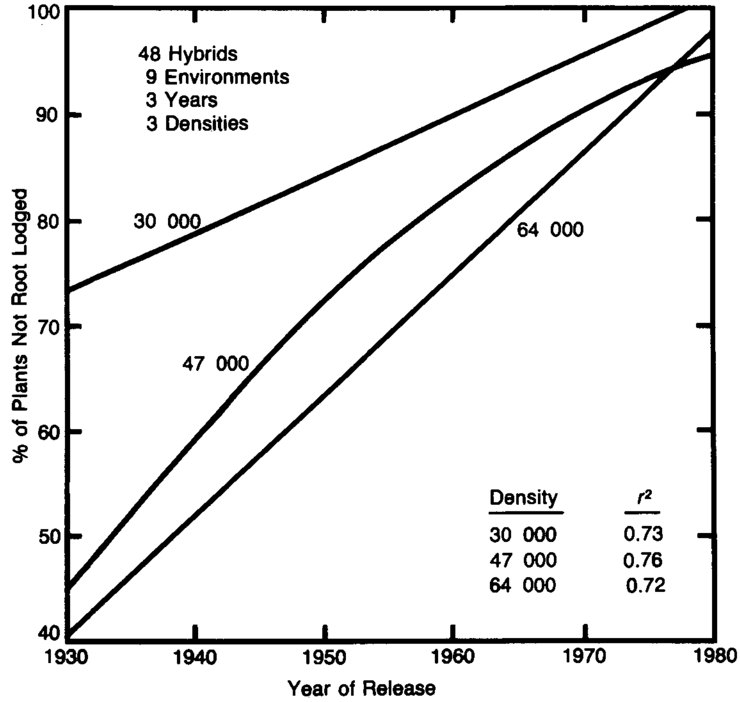

Fig. 2–4. Regressions of percent of plants not root lodged at each density on year of hybrid release, experiment 1. r^2 = coefficient of determination for each regression.

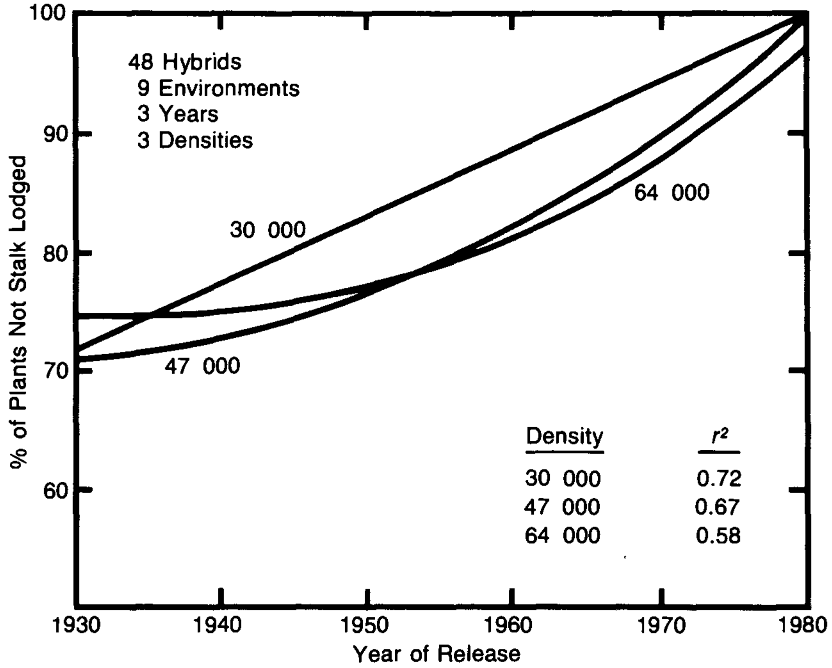

Fig. 2–5. Regressions of percent of plants not stalk lodged at each density on year of hybrid release, experiment 1. r^2 = coefficient of determination for each regression.

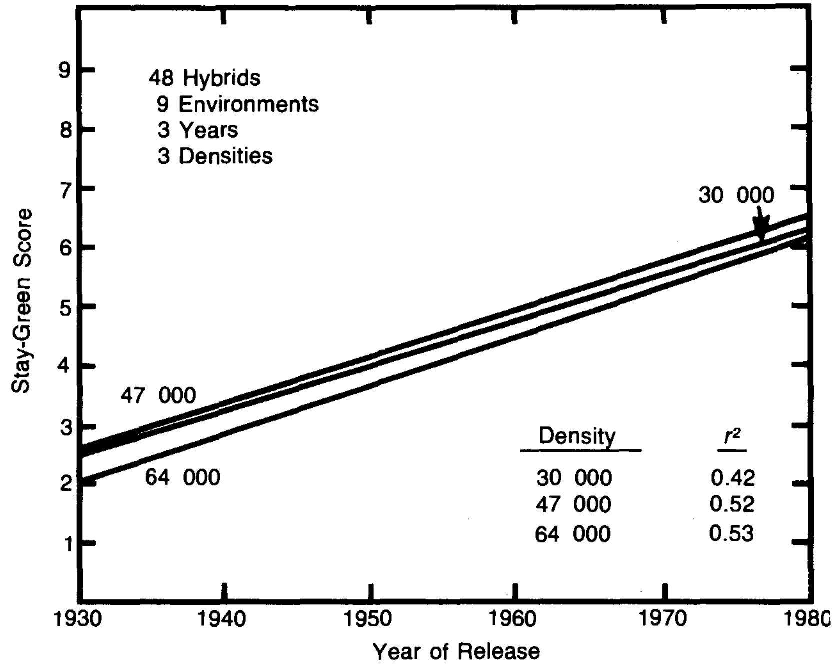

Fig. 2–6. Regressions of stay-green scores at each density on year of hybrid release, experiment 1. r^2 = coefficient of determination for each regression.

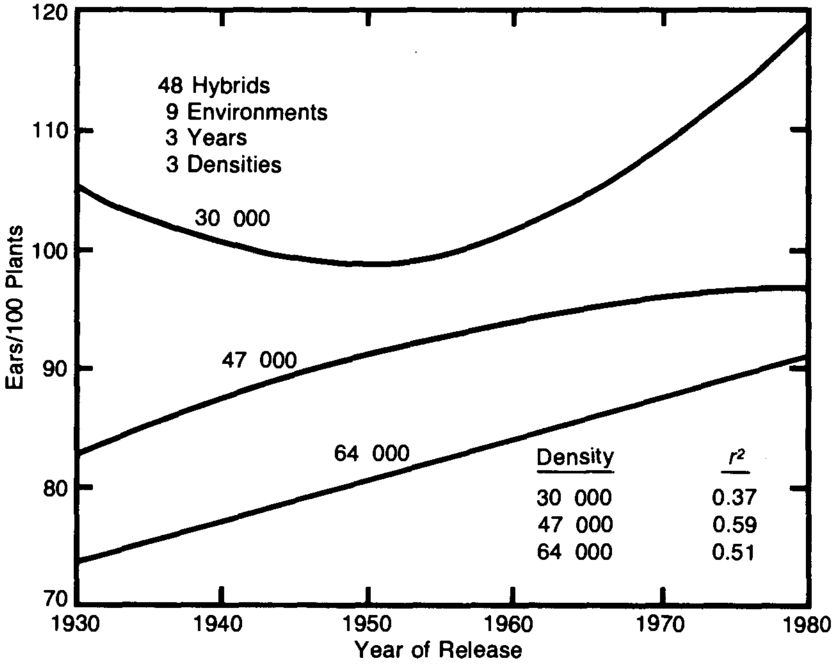

Fig. 2-7. Regressions of ears per 100 plants at each density on year of hybrid release, experiment 1. r^2 = coefficient of determination for each regression.

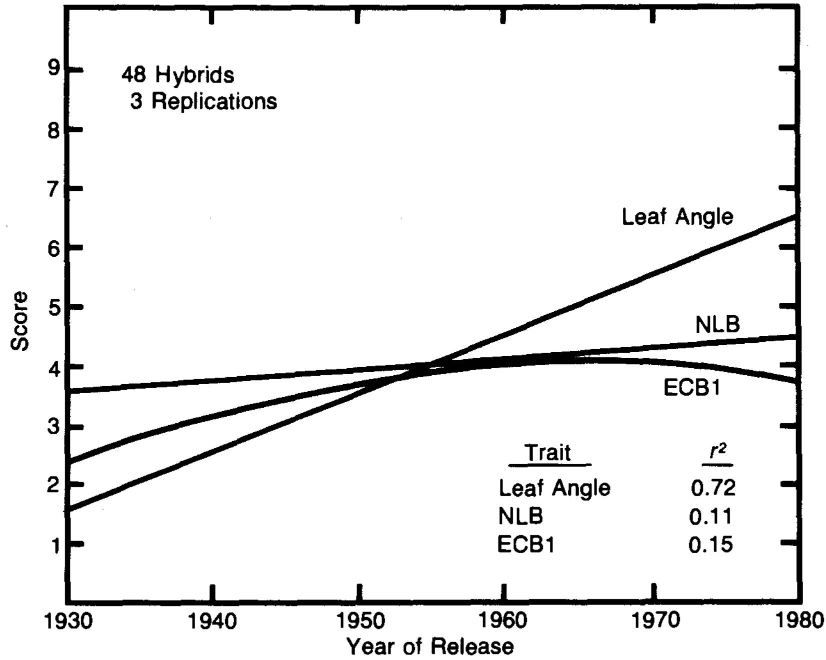

Fig. 2-8. Scores for upright leaf angle, resistance to northern corn leaf blight (*NLB*), and tolerance to first-generation European corn borer (*ECB1*) regressed on year of hybrid release (data from experiment 1). r^2 = coefficient of determination for each regression.

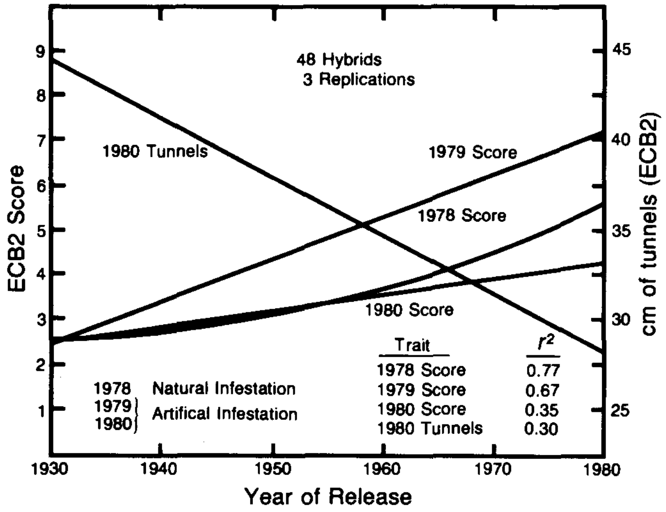

Fig. 2–9. Three scores for tolerance to second-generation feeding of European corn borer (*ECB2*) and centimeters of tunnels made by European corn borer regressed on year of hybred release. Data from experiment 1 in 1978, 1979, and 1980. (Data from 1980 gathered by W. D. Guthrie, Corn Insects Res. Unit, USDA-ARS and Iowa State Univ., Ankeny.) r^2 = coefficient of determination for each regression.

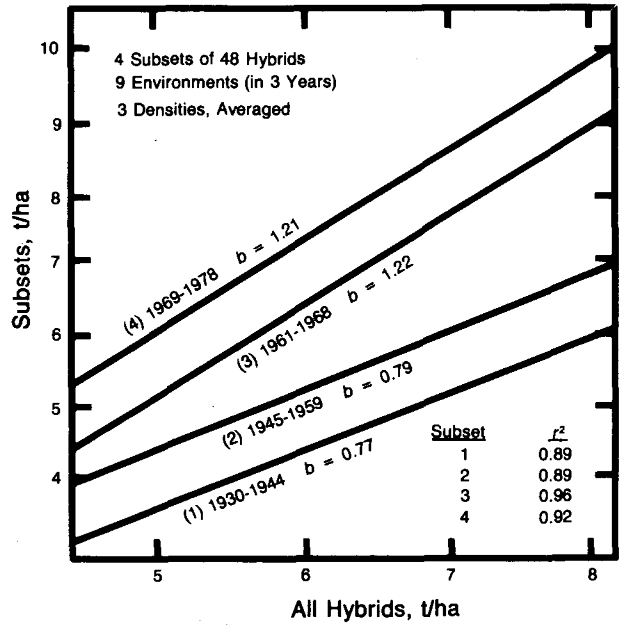

Fig. 2–10. Grain yields averaged over densities of four subsets of hybrids in experiment 1 regressed on mean yield per location using nine locations in 3 years. r^2 = coefficient of determination for each regression. b = regression coefficient in the linear regression equation $Y = a + bx$.

artificial infestation and whether measured by scoring for external symptoms or by splitting stalks to measure tunnel lengths (Fig. 2–9). Low r^2 values for some of these regressions indicate much variability among hybrids within a given release period. Scores for 1978, the year of heavy natural infestation, showed the most uniform improvement among hybrids over the years.

REGRESSIONS OF SUBSETS ON RANGE OF YIELD LEVELS

In answer to the question "Can the new hybrids yield as well as the old hybrids in low yield environments?", the 48 entries were divided into four equal subsets according to year of release: 1930 to 1944, 1945 to 1959, 1960 to 1968, and 1969 to 1978. Yields of the subsets averaged over densities were regressed on average yields of all 48 entries at each of the nine locations (Fig. 2–10).

Actual yields per subset in the nine environments ranged from a low of 3.4 t/ha for the 1930 to 1944 subset at one location in 1980 up to 9.4 t/ha for the 1969 to 1978 subset at two locations in 1979. Fertility was adequate to high at all locations; low yields usually were caused by heat and drought stress in some of the locations in 1978 and 1980. Barren plants, premature death, and stalk lodging usually were consequent to the heat and drought stress.

Regression analysis showed that at all yield levels the newer the hybrids in a subset, the higher the average yield of the subset (Fig. 2–10). High r^2 values indicated close agreement of subset means with the calculated trend lines. The advantage of the new hybrids was greatest at the higher yielding locations, but the new hybrids also gave the highest yields at the lower yielding environments. An interesting coincidence is the very close agreement of regression coefficients for subsets 1 and 2 and for subsets 3 and 4. A large advance in maximum yield potential seems to have occurred when hybrids in subset 2 were replaced by those in subset 3, and this gain was maintained in subset 4.

The newest subsets had the least root lodging at all levels of root lodging (Fig. 2–11). They showed the greatest advantage, however, at locations with the most root lodging. The actual number of root-lodged plants varied from a high of 58% at one location in 1979 for the 1930 to 1944 subset to a low of 0% at one location in 1980 involving the 1961 to 1968 and 1969 to 1978 subsets.

Comparisons of subsets for resistance to stalk lodging showed that the greatest advantage for the newest hybrids was at locations with the most stalk lodging (Fig. 2–12). The number of stalk-lodged plants varied from a high of 55% in 1979 for the 1930 to 1944 subset to a low of 1% at three locations in 1980 for the 1969 to 1978 subset.

REGRESSIONS AND SOIL FERTILITY LEVELS

Figures 2–13 and 2–14 summarize yield results for the two experiments that compared hybrids from different eras under several N regimes. In both experiments within a given N rate, the newest hybrids gave the highest yields. In both experiments, the interaction of hybrids × N rates was not significant. These data indicate that when yields are low because

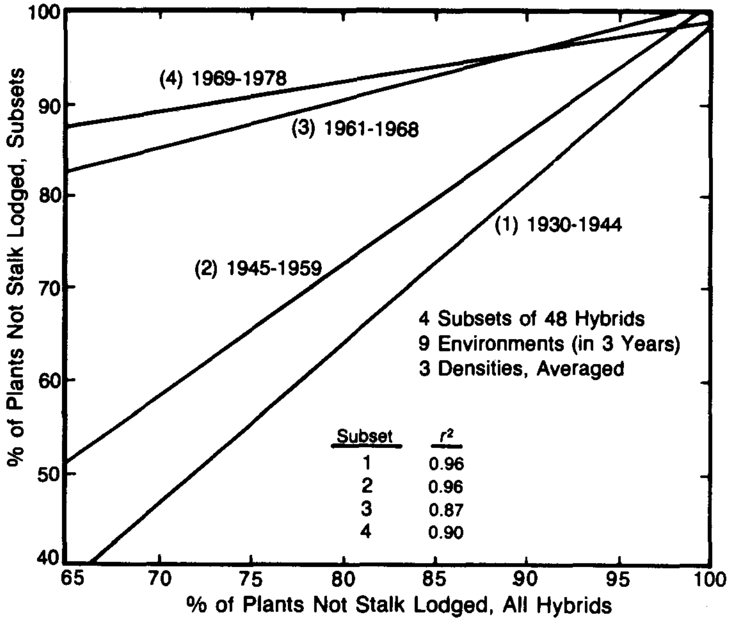

Fig. 2–11. Percent of plants not root lodged averaged over densities of four subsets of hybrids in experiment 1 regressed on mean percent of plants not root lodged at each location using nine locations in 3 years. r^2 = coefficient of determination for each regression.

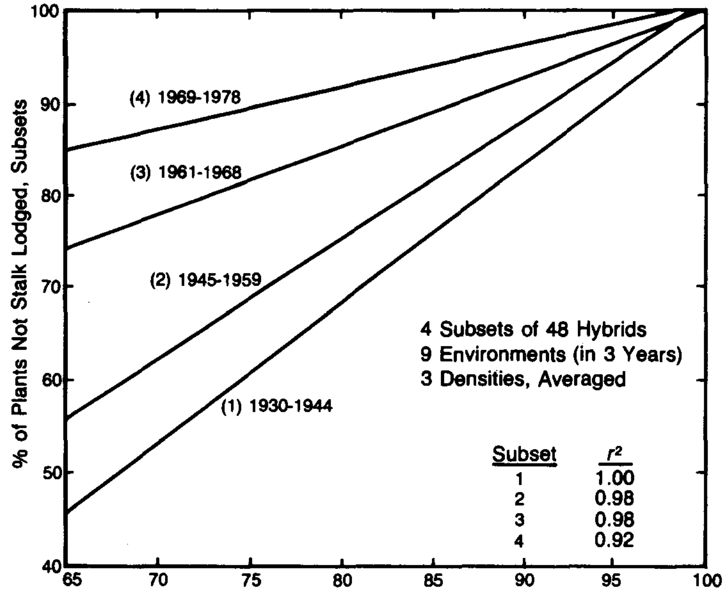

Fig. 2–12. Percent of plants not stalk lodged averaged over densities of four subsets of hybrids in experiment 1 regressed on mean percent of plants not stalk lodged at each location using nine locations in 3 years.

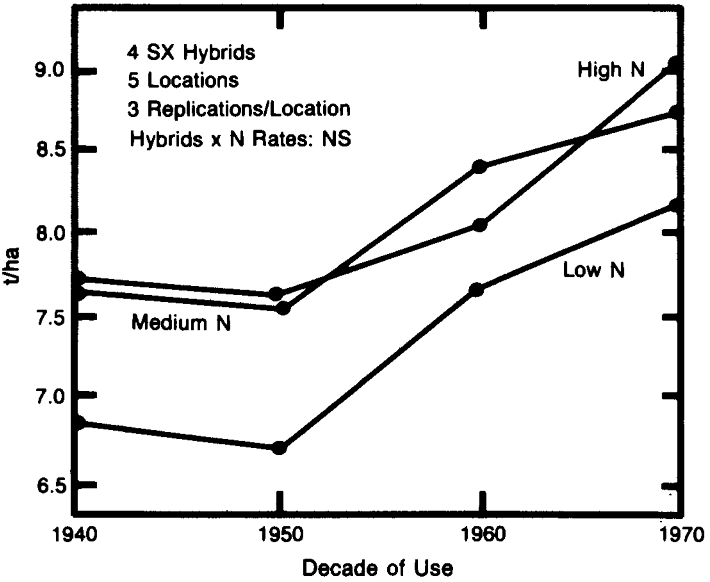

Fig. 2–13. Grain yields of four single cross (*SX*) hybrids representing four decades at three fertility levels. Rates of nitrogen (N) application were approximately 70, 130, and 200 kg/ha. Yield trials grown at five locations using three replications per location. The interaction of hybrids × rates of N was not significant (NS).

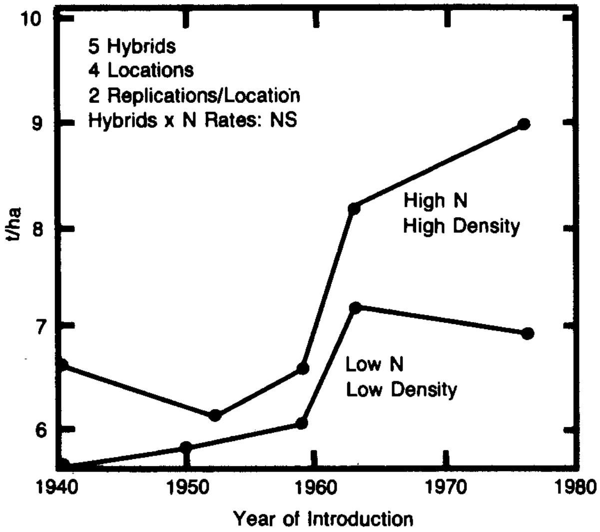

Fig. 2–14. Grain yields of five hybrids introduced from 1940 through 1978 at high nitrogen (N) levels and high density (ca. 215 kg N/ha and 54 000 plants/ha) and at low N levels and low density (ca. 70 kg N/ha and 35 000 plants/ha). Data abstracted from orthogonal test of five hybrids × two densities × three N rates (four locations, two replications). Mean squares for hybrids × N rates and hybrids × densities × N rates were not significantly greater than appropriate error mean squares (NS = not significant).

of N deficiency, newer hybrids still will outyield older ones. The experiments also showed that the new hybrids were greatly superior to the old hybrids in resistance to premature death and to stalk lodging at low as well as high soil N levels. These experiments are corroborated by a similar but independent experiment conducted in 1980 by R. M. Castleberry (1981. Personal communication. DeKalb-Pfizer Genetics, Inc., DeKalb, Ill.) with a series of 20 hybrids and open pollinates. The open pollinates were used to represent maize of the 1930s; the hybrids were representative of those released by DeKalb AgResearch from the late 1930s to the 1980s. Castleberry's experiment showed that the DeKalb hybrids have continually improved in yield over the past 50 years and that the higher yield potential of the newer hybrids was expressed at very low as well as very high levels of soil fertility. The advantage of the new hybrids was greatest at high levels of soil fertility.

Experiment 2: Single Crosses

ANALYSES OF VARIANCE

Mean values of the five 10-year sets showed significant variation for all measured or scored traits. The first- and second-order interactions of diallel means with plant densities and environments usually were significant for environmentally sensitive traits such as yield and standability. Interactions of diallel means with plant densities and environments usually were not significant for highly heritable traits such as height and maturity.

CORRELATIONS

Significant positive correlations were demonstrated at each density between decade of use and grain yield, resistance to root and stalk lodging, favorable stay-green score, ears per plant, and resistance to northern corn leaf blight. Significant negative correlations were found between decade of use and plant and ear height and flowering date. Correlations were low and usually not significant for decade of use with percent of undropped ears, grain moisture, or seedling vigor score.

REGRESSIONS

Yields were still ascending in the 1970s when comparisons were made at medium and high densities, but they showed signs of leveling off after the 1950s in trials grown at the lowest density (Fig. 2–15). The diallels made from the oldest inbreds made their highest yields at the lowest density. The diallels made from the newest inbreds generally made their highest yields at the highest density. These results agree with those for the commercial hybrids of experiment 1. An estimate of amount of increase in yield attributable to genetic improvement can be computed from these data. With the use of the rationale imposed on experiment 1, genetic improvement was 73 kg ha^{-1} $year^{-1}$.

Root and stalk strength were still improving in the 1970s, although gains in stalk strength ascended at a slower rate after the 1950s (Fig. 2–16 and 2–17). Stay-green scores did not increase after the 1950's (Fig. 2–18). Percent of plants with undropped ears at the low density increased until the 1950s and then stayed level (Fig. 2–19). At the two higher densities, there was no clear trend, although the percent of plants with undropped ears seems to have gone down in the 1970s. Prolificacy, expressed at the low density as ears per plant and at the medium and high densities as percent not barren, increased over time (Fig. 2–20).

The newer single crosses outyielded the older ones in low- as well as high-yield environments (Fig. 2–21). These results agree with those of experiment 1. Yields of diallels within locations in experiment 2 ranged from a low of 2.1 t/ha for the 1930s diallel at one location in 1977 to a high of 10 t/ha for the 1970s diallel at one location in 1979. The newer single crosses were more resistant to root and stalk lodging at each test location (Fig. 2–22 and 2–23). The greater the amount of lodging at a given location, the greater the advantage of the newer diallel sets of single crosses. The diallels made from the newest inbreds were more prolific at each location (Fig. 2–24). Prolificacy was expressed either as more ears per plant or as fewer barren plants.

GENERAL COMBINING ABILITY

Each of the 24 inbred lines can be rated within its diallel set according to its general combining ability, the average of its performance in hybrid combinations with the four other inbreds of the diallel. Inbreds with the highest general combining ability for yield averaged across plant densities in each decade set were WF9, PMY, IDT-A, B37, and PH7-A. In second place were KR, LX33, PMD-A, IDT-B, and B73. To avoid bias caused by association of high yields with late maturity, average yield for each inbred was divided by its average grain moisture percent to give a ratio that can be called an "efficiency index." Ratings according to efficiency index again placed WF9, PMY, IDT-A, and B37 in first place in their respective diallels, but OH43-A was the most efficient inbred in the 1970s diallel. Second place rankings for efficiency in each diallel went to 38-11, LX33, KR-B, IDT-B, and B73.

Experiment 3: Inbreds

ANALYSES OF VARIANCE

Mean values of the inbred sets for each decade showed highly significant variation for all measured and scored traits. Interactions of decade means with environments usually were significant for each trait. Interactions of decade means with plant densities usually were not significant.

CORRELATIONS

Inbreds were significantly improved over years for grain yield, root and stalk strength, ears per plant, and resistance to northern corn leaf blight. Stay-green scores, percent of undropped ears, and seedling vigor improved slightly on the average, but correlations with decade of use

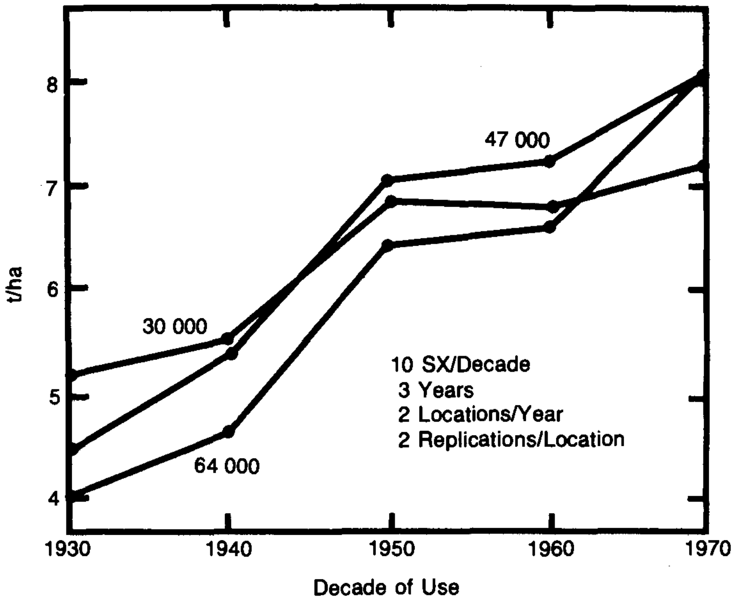

Fig. 2-15. Mean grain yields of five sets of single cross (*SX*) diallels at 30 000, 47 000 and 64 000 plants/ha. Data are from experiment 2.

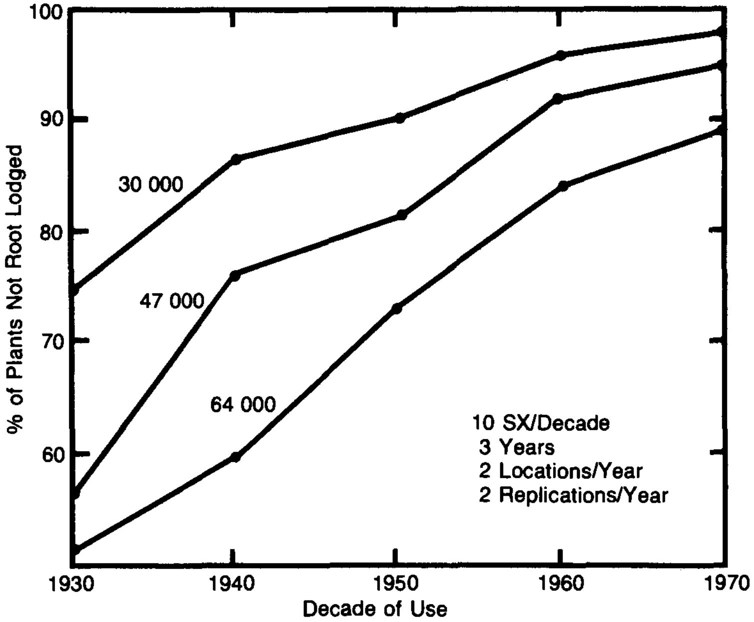

Fig. 2-16. Mean percent of plants not root lodged of five sets of single cross (*SX*) diallels at 30 000, 47 000, and 64 000 plants/ha. Data are from experiment 2.

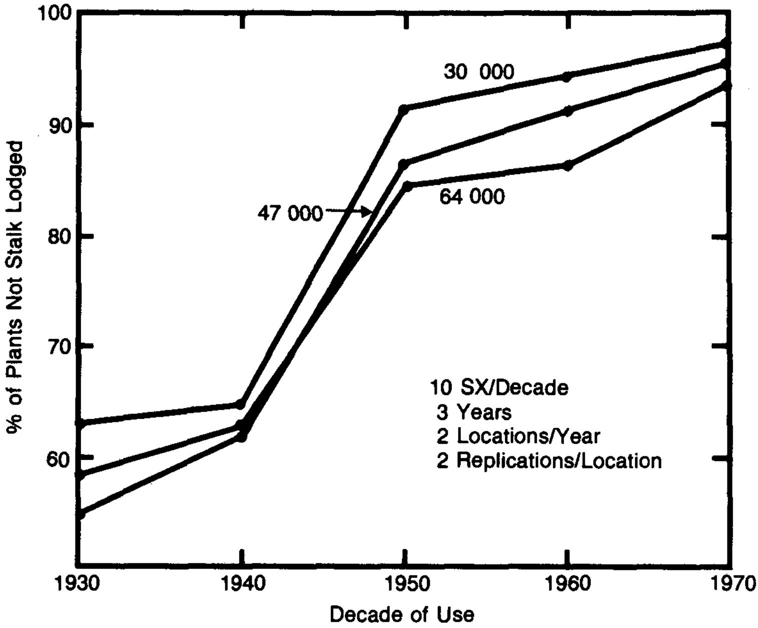

Fig. 2-17. Mean percent of plants not stalk lodged of five sets of single cross (*SX*) diallels at 30 000, 47 000 and 64 000 plants/ha. Data are from experiment 2.

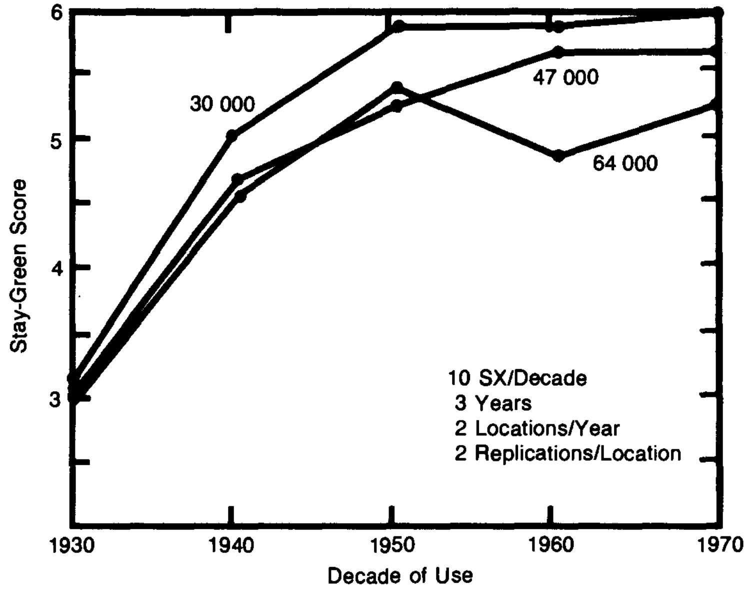

Fig. 2-18. Mean stay-green scores of five sets of single cross (*SX*) diallels at 30 000, 47 000 and 64 000 plants/ha. Data are from experiment 2.

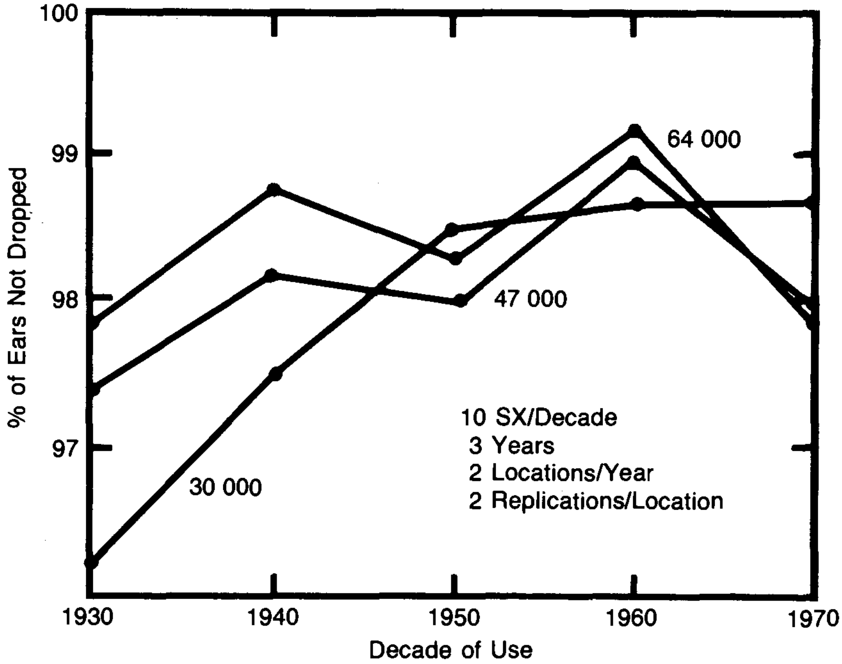

Fig. 2–19. Mean percent of ears not dropped of five sets of single cross (*SX*) diallels at 30 000, 47 000, and 64 000 plants/ha. Data are from experiment 2.

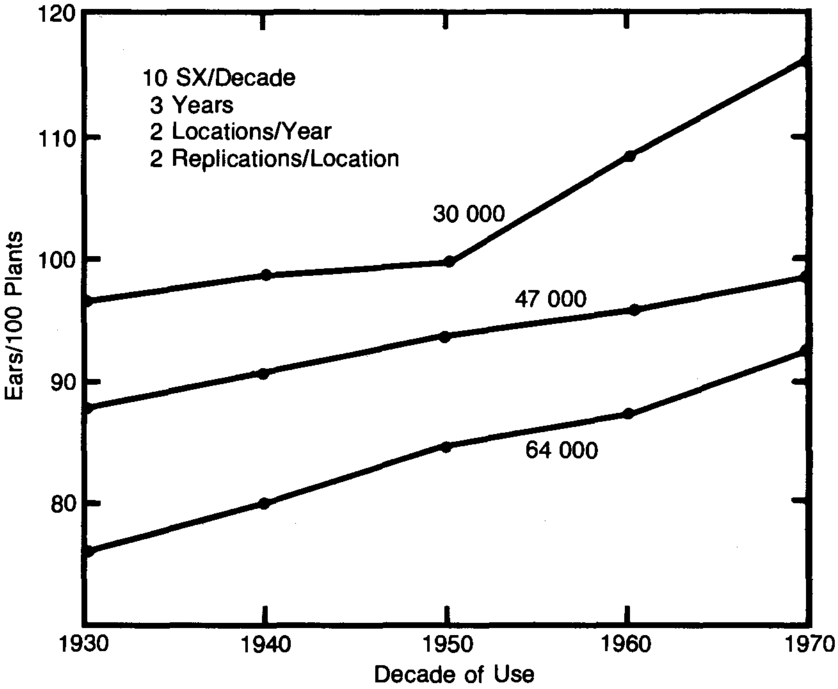

Fig. 2–20. Mean number of ears per 100 plants of five sets of single cross (*SX*) diallels at 30 000, 47 000, and 64 000 plants/ha. Data are from experiment 2.

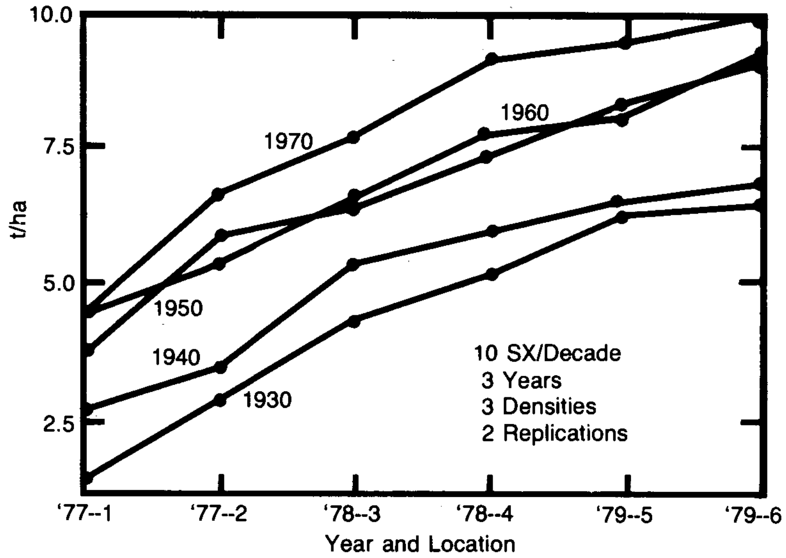

Fig. 2-21. Mean grain yields averaged over three densities of five sets of single cross (*SX*) diallels in six environments. At bottom, where year and location are numbered, the first two digits are the year and the last digit is the location number. Year-locations are arranged in order of successively larger yields of the 1930s diallel.

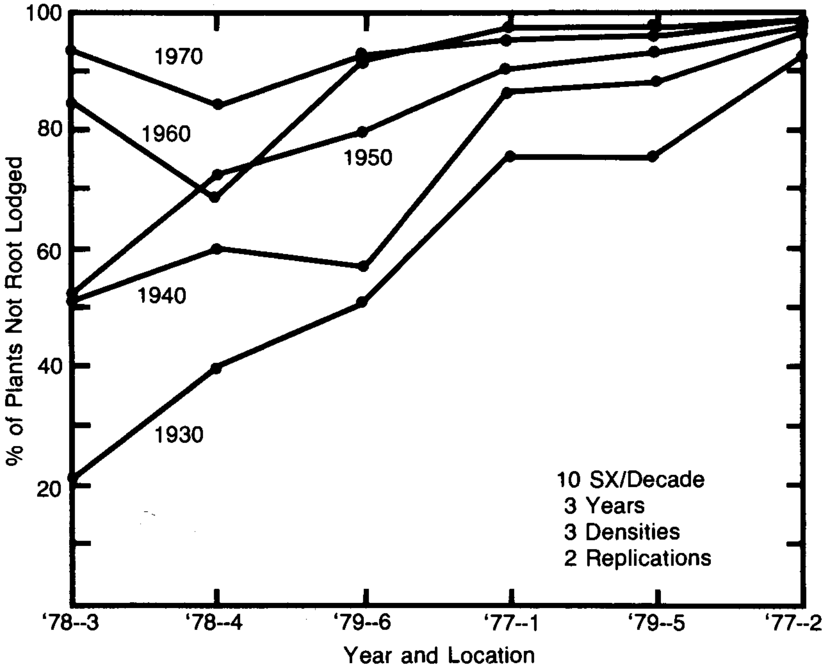

Fig. 2-22. Mean percent of plants not root lodged averaged over three densities of five sets of single cross (*SX*) diallels in six environments. At bottom, where year and location are numbered, the first two digits are the year and the last digit is the location number. Year-locations are arranged in order of successively larger percentage values of the 1930s diallel.

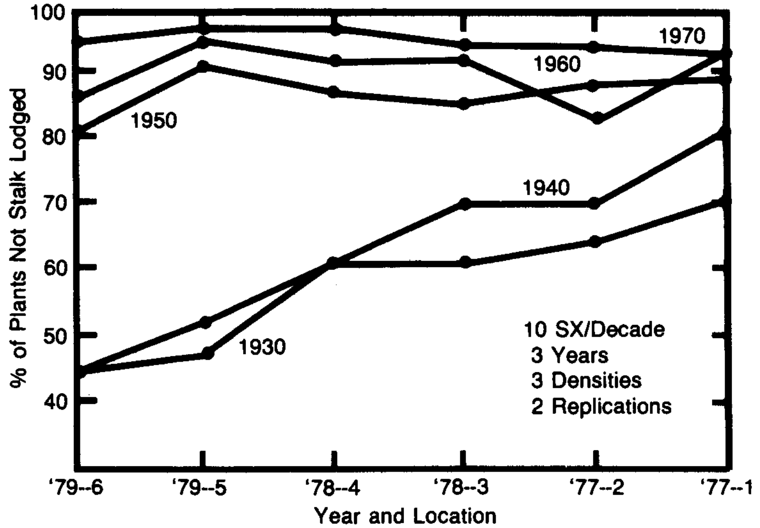

Fig. 2-23. Mean percent of plants not stalk lodged averaged over three densities of five sets of single cross (*SX*) diallels in six environments. At bottom, where year and location are numbered, the first two digits are the year and the last digit is the location number. Year-locations are arranged in order of successively larger percentage values of the 1930s diallel.

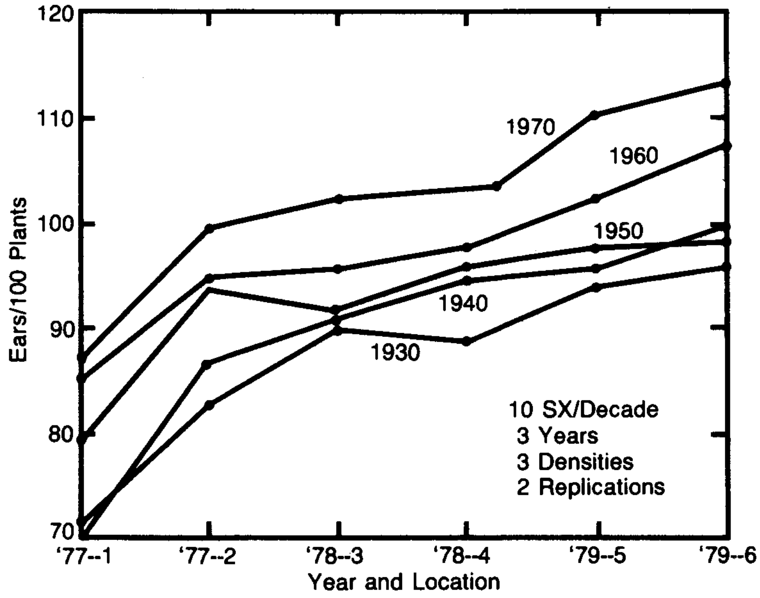

Fig. 2-24. Mean number of ears per 100 plants averaged over three densities of five single cross (*SX*) diallels in six environments. At bottom, where year and location are numbered, the first two digits are the year and the last digit is the location number. Year-locations are arranged in order of successively larger ears per 100 plant values of the 1930s diallel.

were low and not significant. The inbreds showed little or no significant directional change through the years in plant height, ear height, or grain moisture percent, but the average flowering date per decade set became significantly earlier over time, although the change was not great.

REGRESSIONS

Several comparisons of inbreds and their single crosses are shown in Fig. 2–25 to 2–32. Data are presented as averages over the three plant densities. Advances in grain yield (Fig. 2–25), root strength (Fig. 2–26), stalk strength (Fig. 2–27) and ears per plant (Fig. 2–28) were made simultaneously in inbreds and their corresponding single crosses, but inbreds and single crosses did not improve at the same rates. The single crosses advanced in yield at a linear rate of 80 kg ha^{-1} $year^{-1}$, whereas the inbreds gained only 50 kg ha^{-1} $year^{-1}$. The single crosses improved in resistance to root lodging at a rate of 0.9 percentage units per year, whereas the inbreds improved at a rate of only 0.3 units per year. The inbreds of the early decades lodged much less than their corresponding single crosses; therefore, the inbreds had a smaller range for improvement. Resistance to stalk lodging improved at a faster rate in the single crosses than in the inbreds (1.0 percentage unit per year vs. 0.5 percentage unit per year). The earlier decade sets of the single crosses lodged much more than the corresponding inbred sets and had more range for improvement. Both

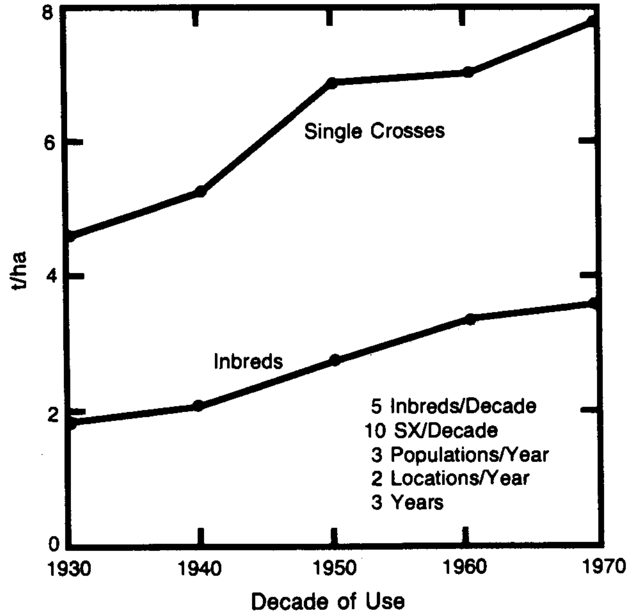

Fig. 2–25. Comparison of single cross and inbred grain yields for experiments 2 and 3. Means of single cross (*SX*) diallels and their inbred parents are averaged over plant densities and environments.

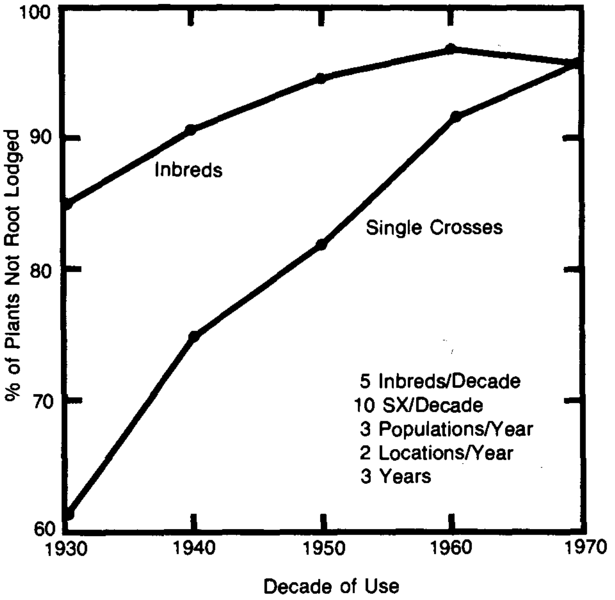

Fig. 2–26. Comparison of percent of plants not root lodged of single crosses and inbreds of experiments 2 and 3. Means of single cross (*SX*) diallels and their inbred parents are averaged over plant densities and environments.

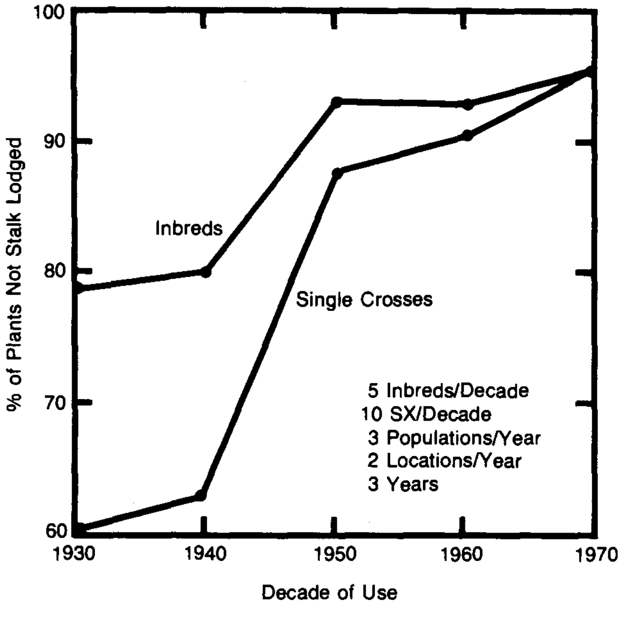

Fig. 2–27. Comparison of percent of plants not stalk lodged of single crosses and inbreds of experiments 2 and 3. Means of single cross (*SX*) diallels and their inbred parents are averaged over plant densities and environments.

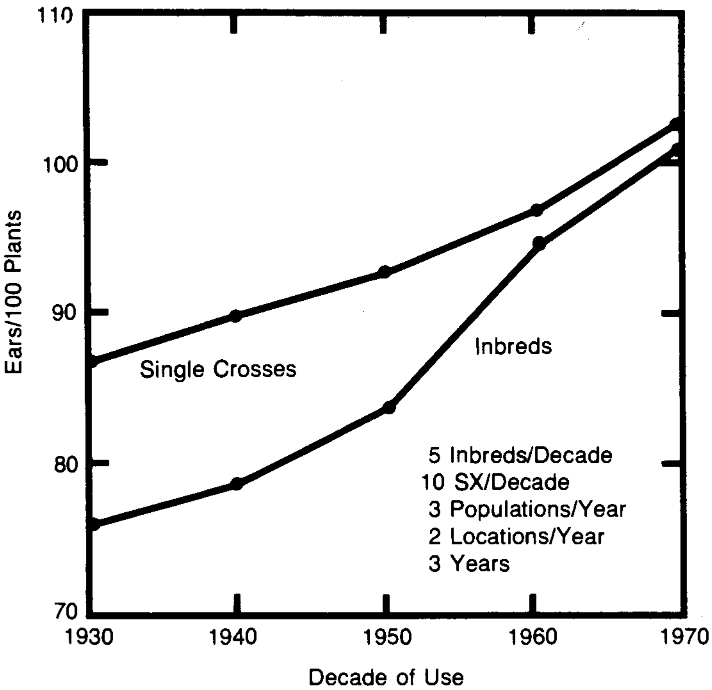

Fig. 2–28. Comparison of ears per 100 plants of single crosses and inbreds of experiments 2 and 3. Means of single cross (*SX*) diallels and their inbred parents are averaged over plant densities and environments.

inbreds and their single crosses made large improvements in resistance to stalk lodging from 1940 to 1950 and relatively small gains thereafter. Inbreds improved at a faster rate than single crosses in ears per 100 plants (0.67 ears 100 plants^{-1} year^{-1} vs. 0.40 ears 100 plants^{-1} year^{-1}), but the older inbreds were more barren than their corresponding single crosses; therefore, the inbreds had more room to make gains.

Single crosses averaged about 134% of the plant height and 138% of the ear height of their inbred parents. The plant height and ear height advantage of single crosses tended to decrease over the decades; i.e., midparent heterosis for height tended to decrease (Fig. 2–29 and 2–30). The trends toward reduction in heterosis for plant and ear height, although slight (about 0.3 cm/year for plant height and 0.4 cm/year for ear height) were statistically significant.

Single crosses averaged 143 fewer growing degree units to anthesis than their inbred parents, a 9% reduction. The newer single crosses showed a statistically significant tendency for reduced heterosis for earlier maturity, measured as growing degree units to anthesis (Fig. 2–31).

The possible trends toward reduced heterosis for height and flowering date maturity may be compared with changes in heterosis for grain yield (Table 2–4, Fig. 2–25). Heterosis for single cross grain yield calculated as percent of midparent yield tended to decrease through the years. On the other hand, heterosis for single cross grain yield calculated as unit gain

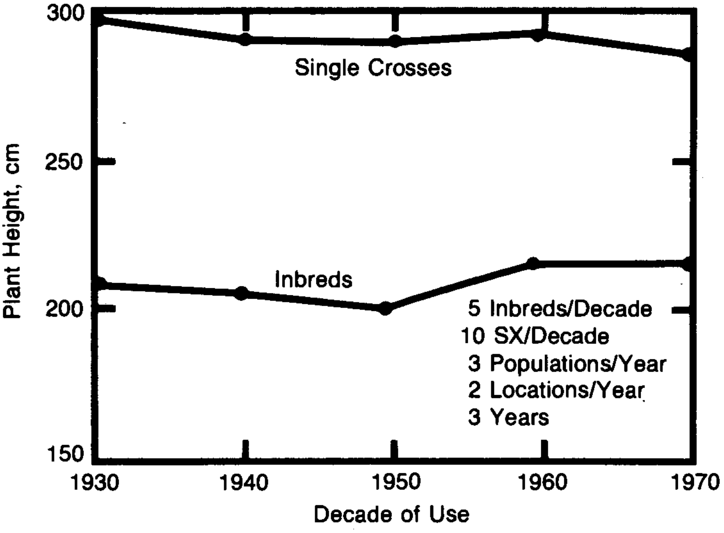

Fig. 2–29. Comparison of plant height of single crosses and inbreds of experiments 2 and 3. Means of single cross (*SX*) diallels and their inbred parents are averaged over plant densities and environments.

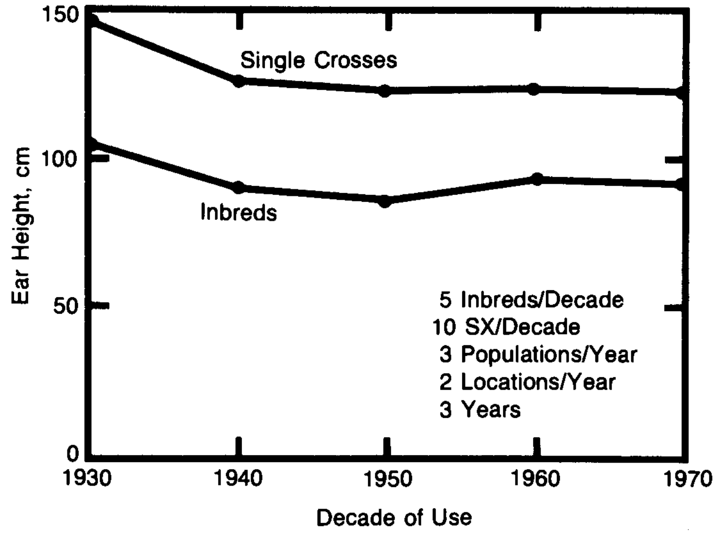

Fig. 2–30. Comparison of ear height of single crosses and inbreds of experiments 2 and 3. Means of single cross (*SX*) diallels and their inbred parents are averaged over plant densities and environments.

over midparent yield increased significantly over the years, at a rate of about 40 kg ha^{-1} $year^{-1}$. These contrasting conclusions appear to be an artifact of the differential rates of increase in yield of inbreds and their hybrids.

Table 2–4. Comparison of grain yields of single cross diallels and their corresponding inbred parents, experiments 2 and 3.

Decade	Single cross means	Inbred means	Single cross mean minus inbred mean	Single cross mean as % of inbred mean
	kg/ha			
1930s	4600	1900	2700	235
1940s	5300	2100	3200	256
1950s	6900	2800	4100	247
1960s	7000	3400	3600	205
1970s	7900	3600	4300	223
$\bar{x}$	6300	2800	3600	233
r†	0.85**	0.86**	0.61**	−0.31*
b‡	80 kg ha^{-1} $year^{-1}$	50 kg ha^{-1} $year^{-1}$	40 kg ha^{-1} $year^{-1}$	−0.8%/year

*,** Significant at 0.05 and 0.01 levels of probability, respectively.

† Correlations of yields or percentages for individual single crosses or inbreds with decades were based on $N = 50$, except $N = 25$ for inbred means.

‡ From linear regressions of yields or percentages on decades. b = regression coefficient in the linear regression equation $Y = a + bx$.

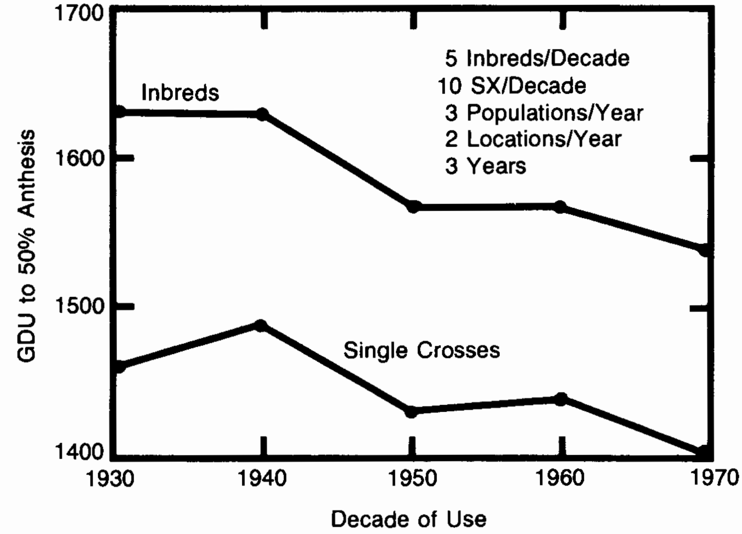

Fig. 2–31. Comparison of growing degree units (*GDU*) to 50% anthesis of single crosses and inbreds of experiments 2 and 3. Means of single cross (*SX*) diallels and their inbred parents are averaged over plant densities and environments.

Average grain moisture percentages of inbreds and their corresponding single crosses were very nearly equal in contrast to flowering date comparisons and changed similarly through the decades (Table 2–5). There seemed to be no trends for inbreds to become either wetter or drier than their corresponding single crosses. Inbreds and their single crosses had lower average percent grain moisture in each successive decade after the 1940s.

Table 2–5. Comparison of mean grain moisture percent of single cross diallels and their corresponding inbred parents, experiments 2 and 3.

Decade	Single cross	Inbred	Single cross as percent of inbred
	% moisture		
1930s	18.8	18.3	103
1940s	20.1	20.1	100
1950s	19.2	19.1	101
1960s	18.9	17.9	106
1970s	18.2	17.7	103
$\bar{x}$	19.0	18.6	102

DISCUSSION

General Comments

The experiments reported herein agree with earlier ones (Hallauer, 1973; Russell, 1974; Duvick, 1977) in demonstrating that genetic yield potential of commercial maize hybrids in the central U.S. Corn Belt has increased continually since the first hybrids were introduced. These experiments agree with the earlier ones in demonstrating continual and large genetic improvement through the years in hybrid standability, stay-green score, and resistance to barrenness concomitant with little or no change in plant height and maturity.

Information on changes in additional traits is available from the present experiments. There was a strong trend toward development of hybrids with a more upright leaf habit. Hybrids showed no change over the years in LAI. Stover dry weight and harvest index tended to increase slightly or not at all depending on the year. The newer hybrids tended to have heavier kernels but fewer kernels per plant. Tolerance to second-generation infestation of European corn borer was significantly improved. Improvements in resistance to northern corn leaf blight and to first-generation infestation of European corn borer, although measurable, were neither large nor continuous.

There was a close relationship between yielding ability and defensive traits such as resistance to premature death, root and stalk lodging, barrenness, and second-generation corn borer. Improvement in these defensive traits likely was an important reason for improvement in yielding ability of the newer hybrids, especially at the higher plant densities. This conclusion is reinforced by the relatively low rate of gain in yield potential when it was measured at the lowest plant density, which presumably puts less stress on individual maize plants. It also is reinforced by the demonstration that the newer hybrids were superior in yielding ability in low-yield environments caused by heat and drought or by low supplies of soil N.

The strong improvement over the years in tolerance to second-generation European corn borer is surprising considering the relatively small number of years (ca. 10) in which artificial rearing and infestation have given opportunity to select for this trait directly. A close agreement between ratings for tolerance to natural infestation of second-generation European corn borer and stay-green scores ($r = 0.80$, $P < 0.01$) and percent of plants not stalk lodged ($r = 0.79$, $P < 0.01$) seems to bear out a prediction made by Dicke about 30 years ago (Dicke, 1954). At that time, Dicke suggested that the best way to select for tolerance to second-generation borer would be to select for better stalk health and strength. Large scale infestation with artificially reared second-generation borers was not an option in the mid-1950s.

The close agreement between trends over time of the commercial hybrids and of the representative single cross diallel sets indicates that continuing improvements in general combining ability of inbred lines may have been a major factor in improving the genetic yield potential of the commercial hybrids. But specific combining ability may have been important also. The design of these experiments does not allow accurate separation of general and specific combining ability components of the commercial hybrids, but it seems likely that specific combining ability may have been an important reason for the fact that yields of the commercial single cross hybrids (1963 to 1978) exceeded the levels predicted by the yield trend of the double crosses (1934 to 1963). In single cross hybrids, breeders can select for specific combining ability with more precision and power than was possible with double cross hybrids.

In some cases, agreement between experiments 1 and 2 was not precise. For example, stalk-lodging resistance and stay-green scores were continually and significantly improved in the commercial hybrids but leveled off after the 1950s in the single cross diallels of widely used inbreds. It appears that in the commercial hybrids the widely used inbreds of the two most recent decades have been supplemented by a range of other inbreds to produce commercial hybrids with improved stalks and stay-green scores.

Improvements in yield, standability, and resistance to barrenness of the inbreds indicate that breeding can make large improvements for these traits in inbreds. This prediction is good news to seed producers because seed production of single cross maize hybrids requires use of high-yielding inbred parents with good standability. The high correspondence between performance of inbred lines and of their single crosses in regard to improvements in yield, standability, and resistance to barrenness agrees with assumptions about the importance of additive gene action for these traits.

Hybrids were simultaneously improved in yield potential and resistance to barrenness and root and stalk lodging, whereas maturity and plant size were held constant. This indicates that the usual negative correlations between yield and standability, yield and early maturity, and yield and short plant height are not impossible obstacles to the plant breeder whose goal is to increase maximum yield potential without sacrificing stress resistance, standability, and optimum plant size and maturity.

The apparent trend toward hybrids with upright leaves may be a byproduct of selection for hybrids with best performance at high densities. One also might have expected that high density selection would have resulted in a trend toward hybrids with lower LAI, but this did not happen. I was surprised at the lack of strong improvement in harvest index. Increases in stover weight seem to have balanced out increases in grain yield. Because plant height and LAI were relatively unchanged over the eyars, it seems that increases in stalk density would be the chief cause of increases in stover weight. Perhaps the observed premature death and pith deterioration of the older hybrids reduced their stover weight and thus increased their harvest index. It is also important to note that in 1980, when heat and drought stress greatly affected grain yields, a small positive correlation was demonstrated between harvest index and year of hybrid release, whereas in 1981, a relatively stressfree year, there was no correlation between harvest index and year of hybrid release.

PREDICTIONS

Will there be further gains in hybrid yield potential? I can extrapolate these curves for at least a few years into the future based on knowledge of the breeding materials now on hand and the power of breeding programs now in place. Gains will continue to be made and will be realized on the farm. Planting rates likely will go up as adventurous farmers successfully explore the yield potential and stress resistance of the new hybrids. Plant breeding experience impels me to caution that gains in hybrid yield potential usually are saltatory. Periods with little progress are interspersed with periods of rapid gains. The gains usually are caused by the introduction of one or two good new inbred lines. Also, not all traits are improved at once. Gains may be made in defensive traits but not in yield, or, new hybrids may be improved in yield but not in defensive traits.

Further progress in maize breeding will depend in large part on choice of breeding systems used to develop improved inbred lines. Although the experiments presented herein are not designed to compare effectiveness of breeding systems, it is perhaps important to note that the two best inbreds of the 1970s diallel were products of the pedigree system of breeding. PH7-A rated first for general combining ability for total yield; OH43-A rated first for general combining ability for efficiency of yield. On the other hand, B73, a product of recurrent selection, was the second best inbred for combining ability both in total yield and in efficiency of yield. Very likely both breeding systems and ingenuous new combinations of them will be useful in the future.

What if maize farming technology changes, especially as a consequence of higher fuel prices? A strong movement toward reduced tillage will likely develop, and the use of N fertilizer in future years may be reduced markedly. Reduced tillage will bring a demand for hybrids with resistance to certain foliar diseases not now considered important. It will increase the need for hybrids with improved spring vigor. Increased emphasis on disease resistance and vigor traits could result in reduced selection pressure for yield potential if total breeding inputs are not increased. Thus, the change in emphasis might slow rates of yield gain in the future. Modern hybrids are increasingly improved in their ability to cope with low levels of soil N; thus, any trend toward reduced N application probably will not require major changes in choice of breeding materials.

How much effort will be needed to maintain present rates of gain? These experiments were not designed to give answers to this question, but obviously the U.S. maize breeding effort, measured in numbers of working maize breeders, has increased manyfold since 1930. I know of no precise figures that might allow one to measure the rate of increase, but observation of my company's effort through the years and comparing it with other organizations indicates probable nationwide personnel increases from 1930 to 1980 of about 4%/year, calculated as percent of the mean for 1930 to 1980. Maize yield potential as measured in experiment 1 has been raised at an average rate of 1.4%/year, calculated as percent of the mean for 1930 to 1980. Thus, we seem to require increasingly greater numbers of maize breeders to maintain a constant rate of improvement in yield. Furthermore, individual maize breeders today have much more energy at their command than in earlier years; the energy is represented by combines, planters, computers, diagnostic laboratories, and insect-rearing facilities. Thus, the cost in units of energy per unit of gain in yield must be much higher today than it was in the past. One can expect that it will be even higher in the future unless ingenious shortcuts are developed. Some shortcuts are devising more efficient conventional breeding schemes, using more precise methods of gene recombination with the help of recombinent DNA technology and tissue culture, and devising other laboratory methods or computer-assisted analyses that will allow replacement of much of the time- and energy-consuming yield trial work.

ESTIMATES OF GENETIC YIELD GAIN

A final exercise, interesting but not as precise as one might wish, is to calculate the percent of total yield gain from 1930 to 1980 due solely to genetic improvement. I have made two different calculations to estimate total yield gain in Iowa during that 50-year period:

1) I have been able to find records of yield trials conducted by my company in numerous locations in central Iowa and just across the border in western Illinois in all but two of the years for 1936 through 1980. These records contain data for all but one of the 47 hybrids included in experiment 1. Yields of these 46 hybrids, regressed against the years in which they were in trial, increased through the years at a linear rate of 103 kg ha^{-1} $year^{-1}$ ($r^2 = 0.70$). The regression calculation gave estimates of achieved mean yields of about 4.9, 6.5, and 9.0 t/ha in yield trials conducted in the years 1935, 1955, and 1980, respectively. In comparison with these estimates, regression calculations for experiment 1, diagrammed in Fig. 2–3, indicated that hybrids released in 1935, 1955, and 1980 yielded in the 1978 to 1980 trials about 4.7, 6.5, and 9.3 t/ha, respectively, at the appropriate density for each era. Thus, yield potentials of the farmer-managed yield trial fields in 1955 and even 1935 may have been nearly as great as they were in 1978 to 1980. Fertile, well-managed land probably was chosen for those early yield trials. One must remember that plant densities at that time were low compared with present practice, and demands on soil fertility, therefore, also were lower than at present.

2) Average maize yields for the entire state of Iowa, according to records furnished by the Iowa Crop and Livestock Reporting Service, increased at a linear rate of 99 kg ha^{-1} $year^{-1}$ ($r^2 = 0.83$) from 1930 through 1980. Yields in central Iowa often are about equal to the state average; therefore, this method may estimate gains in central Iowa with reasonable accuracy.

The two estimates of total yield gain agree quite well, but I believe that the estimate of total yield gain according to method 1, the yield trial estimate, probably is more appropriate for comparisons with the genetic gain estimates of this report. The yield trial estimate of total gains was based on trials grown at sites quite similar to those in my experiments, it used most of the same hybrids, and it was estimated from small plot yield trials similar to those in my experiments. Its value, 103 kg ha^{-1} $year^{-1}$, can be compared with the genetic gains of 92 kg ha^{-1} $year^{-1}$ for the commercial hybrids of experiment 1 and 73 kg ha^{-1} $year^{-1}$ for the single cross diallels of experiment 2. The two comparisons give estimates of the proportion of total yield gain attributable to genetic improvement in each type of hybrid. The estimates are 89% for the commercial hybrids and 71% for the single cross diallels.

The newer hybrids required relatively high plant densities to achieve the yields used in calculating the above rates of gain. Thus, a particular kind of genotype × environment effect is included in the term "genetic component of total yield." It also is likely that severe heat and drought stress in 1977, 1978, and 1980 caused large reductions in yield of the older hybrids and diallels and therefore tilted the regression lines sharply upward. Comparisons of 11 commercial hybrids tested in 1972 and 1973 (Duvick, 1977) and also in the present experiments show that average yields were 12% lower in the 1978 to 1980 trial period, and the regression coefficient was 44% greater (Fig. 2–32).

Seven estimates of genetic yield gain percentages for maize hybrids in Iowa are now on hand (Table 2–6). They range from 33 to 89%. The highest estimate (89%) is from the experiment with the highest proportion of commercial single cross hybrids, all of them new and yielding more than predicted from earlier double cross gains. The single cross hybrids seem to have raised the regression estimate and, thus, the estimate of

Table 2–6. Summary of seven estimates of total yield gain and the genetic component of total yield gain of maize hybrids in central Iowa.

Author	Year reported	Time span	Experiment years	Total gain	Genetic gain	Genetic gain‡
				— kg ha^{-1}	$year^{-1}$ —	%
Darrah†	1973	1930–1970	1930–1970	99	33	33
Russell	1974	1930–1970	1971–1973	78	63	79
Russell	1974	1930–1970	1971–1973	78	49	63
Duvick	1977	1935–1971	1972–1973	88	50	57
Duvick	1977	1935–1972	1972–1973	88	53	60
Duvick	1983	1930–1980	1978–1980	103	92	89
Duvick	1983	1930–1980	1977–1979	103	73	71

† Reported in Hallauer (1973).

‡ Genetic gain as percent of total gain.

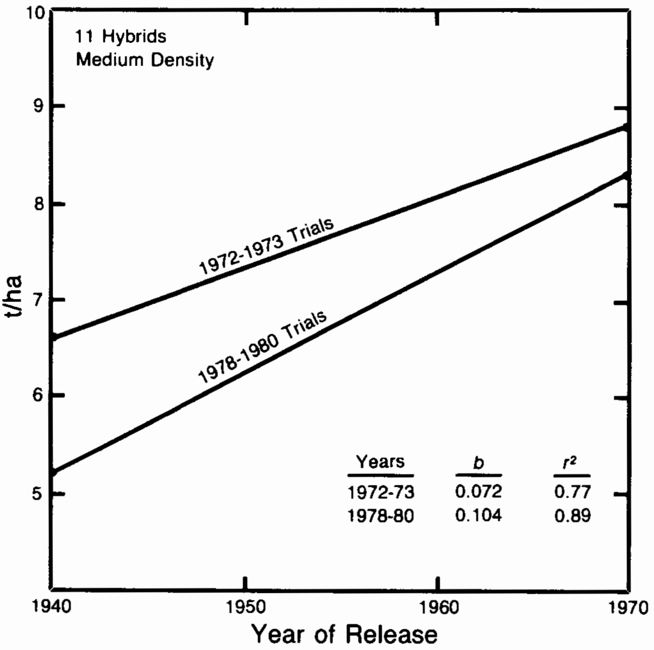

Fig. 2–32. Regressions of hybrid grain yield on year of hybrid release. Eleven hybrids released from 1940 through 1970 as tested in 1972 to 1973 and again in 1978 to 1980 in central Iowa. b = regression coefficient (in t ha^{-1} $year^{-1}$) in the linear regression equation $Y = a + bX$. r^2 = coefficient of determination.

genetic gain. The estimates made by Russell (1974) and Duvick (1977 and this chapter), ranging from 57 to 89%, used high plant densities typical of modern farm practice to allow the newer hybrids to express their yield potential. This points out that the improved yield potential of the new hybrids can be fully expressed only when they are grown with up-to-date cultural techniques. Improvements in maize hybrid genotype and maize culture have been made in concert over the years, and they likely will change together in the future as well. They are a good example of co-evolution, human directed but none the less real, and are susceptible to study and analysis by biologists, sociologists, and economists.

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