GENETIC PROGRESS IN YIELD OF UNITED STATES MAIZE (Zea mays L.)

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ABSTRACT - Maize grain yields in the U.S. started to rise in the late 1930s, concurrent with introduction of hybrids and improved cultural methods. On-farm yield gains averaged 115 kg ha\(^{-1}\) yr\(^{-1}\) during the years 1934-2004. Genetic improvements have been responsible for ca. 50-60% of the on-farm gains, and changes in cultural practices (management) are responsible for the remainder. But because breeding and management interact with each other, neither factor could have raised yields without concurrent and complementary changes in the other. Numerous estimates of genetic yield gain of maize hybrids have shown, without exception, that genetic yield gains during the past 70 years have been positive and linear. Estimates of the average annual gain vary but tend to fall in the range of 65-75 kg ha\(^{-1}\) yr\(^{-1}\). Over the years, hybrids have changed significantly in phenotype, in tolerance to biotic and abiotic stresses, and in genotype as measured by pedigree and molecular markers. Phenotypic changes may indicate improvements in efficiency of grain production (e.g., smaller tassels may release more energy for gain production). Stress tolerance is greatly improved, newer hybrids out-yield the older ones not only in high yield environments but also when trials are subjected to abiotic stress (e.g., heat and drought) or to biotic stress (e.g., insect pests). Absolute heterosis for grain yield has increased over the years to a small extent, in particular when trials are subjected to abiotic stress, but the increase is considerably less than total genetic gain. Yield potential per plant has not increased over the years. Newer hybrids yield more than older hybrids because of continuing improvement in ability of the hybrids to withstand the stress of higher plant density, which in turn is owed to their greater tolerance to locally important abiotic and biotic stresses.

KEY WORDS: Zea mays; Genetic yield gain; Trait changes; Stress tolerance; Genetic diversity; Heterosis.

INTRODUCTION

Maize grain yields in the U.S. began to rise in the late 1930s and have continued to rise up to the present time (Fig. 1) (USDA-NASS, 2004). Gains during the past 70 years have averaged 115 kg ha\(^{-1}\) yr\(^{-1}\) (calculated from USDA-NASS, 2004) but were lower in the first portion and higher in the second portion of this time period (TROYER, 2000). The yield gains were caused by changes in cultural practices and by contributions of plant breeding. The two categories interact; yield gains from changes in cultural practices are dependent on changes in breeding, and vice versa.

Changes in cultural practices

Changes in cultural practices such as weed and pest control, timeliness of planting, and increased efficiency of harvest equipment, have helped to raise yields over the years (e.g., CARDWELL, 1982; EDMADES and TOLLENAAR, 1990; OSTEEN, 2000).

Application amounts of synthetic nitrogen fertilizers increased following World War II. They accelerated markedly after the mid-1960s (from ca. 60 kg ha\(^{-1}\) in 1964 to 140 kg ha\(^{-1}\) in 1985) but leveled off in the 1980s (ERS, 1994; DABERKOW et al., 2000).

Plant density of maize in the U.S. has increased steadily in the U.S., starting in the years following World War II; during the past 50 years, gains in plant density in the central U.S. Corn Belt have averaged about 1,000 plants ha\(^{-1}\) yr\(^{-1}\). Plant density averaged about 30,000 plants ha\(^{-1}\) (or less) in the 1930s; about 40,000 plants ha\(^{-1}\) in the 1960s, 60,000 plants ha\(^{-1}\) in the 1980s, and densities at present are typically 80,000 plants ha\(^{-1}\) or higher in the major maize producing regions of the country (USDA, 1949-1992; DUVICK, 1977, 1984b, 1992; PASZKIEWICZ and BUTZEN, 2001; DUVICK et al., 2004b).
**Genetic changes, brief history**

**Farmer breeding:** Farmer breeders, beginning with the Native Americans who first domesticated maize, have developed thousands of landraces adapted to a multitude of environments as well as with a wide range of morphological and quality traits (GROBMAN et al., 1961; PATERNIANI and GOODMAN, 1977; GOODMAN and BROWN, 1988).

Farmers developed adapted maize open pollinated cultivars (OPCs) for the U.S. Corn Belt states within a few decades after settlement of the region in the early years of the 19th century (HALLAUER and MIRANDA, 1988; WALLACE and BROWN, 1988). Unadapted cultivars (or sometimes crosses of cultivars) were successfully reselected for adaptation to the new region, but after the initial advance, gains in yield were small or non-existent, as evidenced by the lack of gain in U.S. maize yields during the first three decades of the 20th century (Fig. 1) (USDA-NASS, 2004).

**New methods:** New breeding techniques (e.g., simple methods of mass selection, or production of hybrids by crossing two open pollinated cultivars) were proposed and tried in the late 19th and early 20th centuries (see reviews in RICHEY, 1922; SPRAGUE, 1946; RUSSELL, 1991; CRABB, 1993; CROW, 1998). But these methods usually did not increase yields, except when a program such as simple mass selection enabled adaptation to a new environment. Further gains required other methods of selection and breeding.

**Maize hybrids:** Maize hybrids, crosses of inbred lines, were developed in the 1920s and introduced in volume in the 1930s (JENKINS, 1978; RUSSELL, 1993). Their superior performance encouraged their adoption by farmers, and use of hybrids increased rapidly, first in the U.S. Corn Belt and then in all other maize-growing regions of the country (RUSSELL, 1991).

The first two or three decades (1930s through 1950s) of increase in area planted to hybrids corresponded with the initial increases in on-farm maize yield (USDA, 1944-1962; USDA-NASS, 2004) and preceded the significant increases (in the 1960s) in use of synthetic nitrogen fertilizers or chemical control of weeds and insects (USDA, 1956; CARDWELL, 1982; ERS, 1994; DABERKOW et al., 2000; FERNANDEZ-CORNEJO, 2004). One can infer that on-farm yield gains of maize in those early decades (ca. 1930s through 1950s) were owed primarily to genetic gain - to the initial introduction of maize hybrids and then to a continuing succession of improved hybrids.

Likewise, one can speculate that because application amounts of nitrogen fertilizer have not risen on average in recent years (see above discussion), the linear increase in on-farm maize yields during the past two decades owes more to genetic yield gain (improved hybrids) than may have been the case during the 1960s to 1980s period of rapid rise in application amounts of nitrogen fertilizer. Both speculations rest on the assumption of genetic yield gain, which is discussed in the next section.

**GENETIC GAINS IN GRAIN YIELD OF U.S. HYBRIDS**

RUSSELL (1991) summarized 13 independent estimates of genetic yield gains of sequentially released maize hybrids in the U.S. The estimates were reported during the 20-year period 1971 through 1991. All of the experiments showed positive and linear genetic yield gains. Estimates ranged from 33 to 92 kg ha\(^{-1}\) yr\(^{-1}\) with a mean of 66 kg ha\(^{-1}\) yr\(^{-1}\).

Additional estimates of genetic gain in hybrids have been made since Russell's review. DUVICK (1997) stated that an Iowa-adapted time-series of hybrids representing the period from 1930 through 1991 showed a linear gain for grain yield of 74 kg ha\(^{-1}\) yr\(^{-1}\).

A further update extended this time-series through the year 2001; it showed an estimated linear gain of 77 kg ha\(^{-1}\) yr\(^{-1}\) (Fig. 2) (DUVICK et al., 2004b).

Overall, these estimates indicate that linear genetic gains in grain yield have approximated 65 to 75 kg ha\(^{-1}\) yr\(^{-1}\) during the past 70 years of hybrid breeding.
ESTIMATES OF THE CONTRIBUTION OF MAIZE BREEDING TO ON-FARM YIELD GAINS

Russell (1991) listed 13 estimates of genetic yield gain of hybrids as percent of total (on-farm) yield gain. Estimates of genetic gain as percent of total gain varied from 33% to 94%, with a mean of 66%. Examination of the data in Duvick et al. (2004b) provides an estimate of 51% for the contribution of genetics, when trial yields are adjusted to the equivalent of average on-farm yields for Iowa during the period 1930 to 2001 (Duvick, 2005).

These estimates, overall, indicate that hybrid maize breeding during the past six or seven decades has been responsible for about 50 to 60% of the total on-farm yield gain.

CHANGES THAT HAVE ACCOMPANIED GENETIC YIELD GAINS IN HYBRIDS

Genetic gains in grain yield of hybrids have been accompanied by changes in other traits. Duvick (2005) reviewed reports of these changes, and the following sections summarize (and in some cases update and discuss) the changes that have occurred.

FIGURE 2 - 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. From Duvick et al. (2004b). Copyright © 2004 by John Wiley & Sons, Inc. This material is used by permission of John Wiley & Sons, Inc.

Plant and ear traits

Plant and ear height showed irregular trends toward reduction in height (especially for ear height) but trends were weak (Meghji et al., 1984; Russell, 1984; Duvick et al., 2004b).

A trend toward increasingly upright leaves began in the 1970s (Crosbie, 1982; Meghji et al., 1984; Russell, 1991; Duvick et al., 2004b).

Tassel size (e.g., branch number and tassel weight) has decreased consistently over the years since release of the first hybrids (Meghji et al., 1984; Duvick, 1997; Duvick et al., 2004b).

Number of leaves per plant increased from 12.2 in the 1930s to 13.8 in the 1970s, in comparisons of 26 single crosses representing U.S. Corn Belt hybrids of the 1930s, 1950s and 1970s (Meghji et al., 1984). In contrast to these results, leaf number neither increased nor decreased in a time-series (1930 through 1991) of 36 commercial hybrids and one OPC adapted to the west-central Corn Belt (Duvick et al., 2004b).

Leaf area index (LAI) did not change over time in three time-series of hybrids for the west-central U.S. Corn Belt (Crosbie, 1982; Russell, 1991; Duvick, 1997).

Leaf rolling under drought consistently increased in successively newer hybrids in a set of Iowa-adapted hybrids representing the period 1953 to 2001, when the hybrids were grown in a rain-free environment in Chile (Edmeades et al., 2003; Barker et al., 2005). According to Barker et al., “Apparently elite hybrids can reduce radiation interception and water use by leaf rolling, while generating sufficient assimilate flux to the ear to set adequate kernel numbers and conserving water for later in the season.”

Staygreen, also called delayed leaf senescence, or resistance to premature death from unidentified causes, consistently improves in successively newer hybrids (Crosbie, 1982; Meghji et al., 1984; Russell, 1991; Tolenaar, 1991; Duvick et al., 2004b; Valentiniuz and Tolenaar, 2004; Barker et al., 2005).

Number of tillers per 100 plants varied from hybrid to hybrid, but decreased slightly on average in a 1930 to 1991 time-series of hybrids and OPCs for Iowa (Duvick et al., 2004b).

Date of anthesis showed no trend toward earlier or later dates in two unrelated hybrid time-series, each adapted to central Iowa (Russell, 1985; Duvick et al., 2004b).

Date of silk emergence showed little or no change over the decades in absence of abiotic stress...
but in presence of abiotic stress (e.g., high plant density and/or drought) silk emergence was delayed in the older hybrids but relatively unchanged in the newer ones. The older the hybrid, the greater the delay, on average (Russell, 1985; DuVick, 1997).

Anthesis-silking interval (ASI) on average shows a linear trend to shorter intervals over the years, in particular when hybrids are grown under stress such as drought or high density (Crosbie, 1982; Meghji et al., 1984; Russell, 1985; Edmeades et al., 2003; DuVick et al., 2004b; Barker et al., 2005).

Ears per 100 plants (sometimes expressed as “ears per plant”) did not change over the years when hybrid time-series were subjected to low stress, but ears per 100 plants increased over the decades (i.e., barrenness decreased) when hybrids were grown under stress of high density (Crosbie, 1982; Russell, 1985; DuVick et al., 2004b).

Newer hybrids had a longer period of grain-fill, calculated as the time from silk emergence to black layer (physiological maturity) (Crosbie, 1982; Meghji et al., 1984; Cavalieri and Smith, 1985; Russell, 1985). The newer hybrids flowered at approximately the same time as the older hybrids, but exhibited faster dry-down at the end of grain-fill, and so had little or no increase in grain moisture percentage at harvest time, despite a longer period of grain-fill.

Hybrids exhibited a general trend to increased weight per kernel (but no increase in number of kernels per ear in the one series where this was measured) (Crosbie, 1982; Russell, 1985; DuVick, 1997; Edmeades et al., 2003; Barker et al., 2005).

Grain protein percentage declined consistently in a series of 36 hybrids and one OPC for central Iowa, spanning the period 1930 to 1991 (DuVick, 1997).

Grain starch percentage increased consistently in a series of 36 hybrids and one OPC for central Iowa, spanning the period 1930 to 1991 (DuVick, 1997).

Harvest index (HI) did not change consistently over time according to three reports: (Crosbie, 1982; Meghji et al., 1984; Russell, 1985), but in two other examinations (DuVick, 1997; DuVick et al., 2004b) HI improved to a small degree in successive hybrids, in particular at higher plant densities. The superior HI of the newer hybrids at higher plant densities was not because of increased HI per se in the newer hybrids, but because of reduced HI in the older hybrids - a result of barrenness induced by stress.

Resistance to root lodging

Hybrids improved over the years in resistance to root lodging although some examinations showed a tendency for improvement to level off at approximately 95 to 100% not-lodged plants (Russell, 1974, 1984; DuVick, 1977, 1984b, 1992, 1997; DuVick et al., 2004a).

Resistance to stalk lodging

Stalk lodging resistance improved consistently over time but as with root lodging, some trials showed a tendency to level off at 95 to 100% not-lodged plants (Russell, 1974, 1984; DuVick, 1977, 1984b, 1992, 1997; DuVick et al., 2004a).

Tolerance to abiotic stress

An Iowa-adapted hybrid time-series showed linear increases in yield in a “very cool and wet season” and also in a “hot and dry” season (Fig. 3) (DuVick, 1997; DuVick et al., 2004b). The “very cool and wet season” was one of the wettest on record for the state of Iowa (Corrigan, 2003; Iowa State University, 2004).

Genetic yield gains over time were expressed in drought as well as in favorable growing seasons (Russell, 1974, 1991; Castleberry et al., 1984; DuVick, 1997; Edmeades et al., 2003; DuVick et al., 2004b; Barker et al., 2005). On average, the newer the hybrid, the greater was its drought tolerance.

When several hybrid time-series were grown at

![Figure 3 - Grain yield per hybrid regressed on year of hybrid introduction for trials grown in 1992, 1993, and 2001. Growing season was highly favorable in 1992, excessively wet and cold in 1993, and hot and dry in 2001. Yield per hybrid is for the density giving the highest average yield. From DuVick et al. (2004b).](https://example.com/figure3.png)

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lower and higher levels of nitrogen fertilizer, in each case the newer the hybrid the greater the yield, at all levels of fertilizer application (CASTLEBERRY et al., 1984; DUVICK, 1984b; CARLONE and RUSSELL, 1987). The yield advantage of newer hybrids (compared with older ones) at lower levels of nitrogen fertilizer application indicates that nitrogen use efficiency has improved over the decades.

DUVICK (2005) indicated yield trial results can be categorized according to average yield at each test site, assuming that the lower the yield at a given site (in absence of obvious disease or insect problems) the greater the amount of “unspecified” abiotic stress. A stability analysis of the kind proposed by EBERHART and RUSSELL (1966) can be used to compare yield response of individual hybrids, or of groups of hybrids such as those released in a given decade. Mean yields of hybrid groups at each test site can be regressed on mean yield of all hybrids at each test site.

A review by RUSSELL (1991) of several experiments that applied this analysis, and a report by DUVICK et al. (2004b) that applied the analysis, showed that, in nearly every instance the newer the hybrid group the higher the yield, at all sites (e.g., Fig. 4). The yield advantage of the newer hybrids (compared with the older hybrids) at the lower yield sites indicates that the newer hybrids were more tolerant of “unspecified abiotic stress” than were the older hybrids. And, conversely, the yield advantage of the newer hybrids at the higher yield sites showed that they also were more responsive to favorable growing conditions.

**Tolerance to biotic stress**

A 1930-1991 time-series of hybrids showed linear gains in resistance to second generation European corn borer (*Ostrinia nubilalis* Hubner) (ECB2), but not to first generation borer (ECB1) (DUVICK, 1997). This series contained no transgenic hybrids; conventional breeding was responsible for the gains.

In recent years (starting in 1996), seed companies have commercialized transgenic maize hybrids that are resistant to both generations of ECB (PEFEROEN, 1992; TRAORE et al., 2000), and more recently (starting in 2003) to two different species of rootworm (*Diabrotica barberi* Smith & Lawrence, and *Diabrotica virgifera virgifera* LeCont) (JAMES, 2003; RICE et al., 2003). It is too early to know how much contribution to yield might be produced by these transgenic changes over the long term, although data now on hand indicate they can add to yield in times of heavy insect infestation but not if infestation is low and/or inconsequential (RICE, 1997; GIANESSI and CARPENTER, 1999; DILLEHAY et al., 2004). Interestingly, if yield of wholesome grain is an important goal, transgenic hybrids such as these can give safer grain (for either food or feed) in some situations. CLEMENTS et al. (2003) say “Results suggest that Bt hybrids can reduce fumonisin concentration in grain during seasons when ECB [European corn borer] is favored, but not during seasons when CEW [corn ear worm, *Heliothis zea* Boddie] is favored”. The transgenic hybrids in this study were less effective on CEW than on ECB.

DODD (2000), states that during the past 40 years at least 14 diseases of maize have had significant increase in importance in the U.S., although not all have been persistent or widespread. Breeding for disease resistance enhances yields most strongly if the disease is active on susceptible hybrids (as is also the case with insect resistance). This interaction complicates efforts to correlate success in breeding for disease resistance with advances in hybrid yielding ability. As RUSSELL (1993) says “Selection for disease resistance has been an integral component of maize breeding for many years, yet there are few data reflecting directly how the success of this selection affects grain yield.”
Response to changes in plant density

On-farm plant density has risen without pause in the U.S., starting in about the 1950s (see discussion in earlier section). Numerous examinations show that older hybrids yield more at lower plant densities (the on-farm densities of their time, and for which they were bred), and newer hybrids yield more at higher plant densities (on-farm densities of their time and for which they were bred) (e.g., Fig. 5) (Duvick, 1977, 1984b, 1992; Russell, 1991).

Studies of a hybrid time-series for central Iowa indicate that yield potential per plant has not increased over the years. When the hybrids are grown at the very low plant density of 10,000 plants ha⁻¹ (which provides a nearly stress-free environment and enables very high yields per plant) yields per plant (and thus yields per hectare) do not increase to any significant degree over the years (e.g., Fig. 5) (Duvick, 1997; Duvick et al., 2004a,b). Continuing gains in yield per unit area are owed not to more grain per plant, but rather, to adaptation of hybrids to continually higher plant densities, thus providing more grain-bearing plants per hectare. Today's hybrids at today's plant densities make about the same amount of grain per plant as was made by the older hybrids at the lower plant densities of their time (Duvick, 2005).

Other physiological traits

Barker et al. (2005) examined a time-series of 18 commercial hybrids (1953-2001) adapted to central Iowa, growing them in a rain-free environment in Chile with application of managed drought stress at various stages of development. They found that canopy temperature under drought stress consistently decreased, going from older to newer hybrids. They suggested that the trend to lower canopy temperature under drought stress might result from the lower radiation intensity on the more upright leaves of modern hybrids, or from a greater capacity by these hybrids to capture soil water.

Parentage, molecular markers, and genetic diversity

Although at the present time one cannot ascribe specific gains in performance over time to specific changes in pedigree, or in gene combinations (and/or gene regulation), one can chart some of these changes with hope that future advances in molecular biology will be able to show how such changes have (or have not) helped to improve performance of hybrids over time.
continuing volatility of genotypes over the decades (“genetic diversity in time”).

Analysis by multidimensional scaling of allele polymorphisms among the parental inbred lines of the hybrids separated the older inbred lines (usually parents of double cross hybrids) from the newer inbred lines. The newer lines sorted into two heterotic groups, called Stiff Stalk and Non Stiff Stalk. This separation of the newer lines agrees with the observation that breeders, using pedigree information and empiricism (practical experience), have established two breeding pools to balance important traits in the final hybrids, as well as to improve efficiency of seed production (Stiff Stalk for seed parents and Non Stiff Stalk for pollinator parents).

**Heterosis: hybrid and inbred performance**

**DUVICK (2005) reviewed several studies (DUVICK, 1984b, 1999; MEGHJI et al., 1984; DUVICK et al., 2004b) that examined the contribution of heterosis to improvements in yield of U.S. maize hybrids. He concluded that**

1. Absolute heterosis for grain yield has increased over the years to a small extent (more so under abiotic stress) but its annual gain is less (sometimes much less) than total genetic gain in hybrid yield. Inbred and single cross yields have each increased over the decades, but single cross yield has advanced to greater degree (Fig. 7). Absolute heterosis is defined as “yield of a single cross minus the mean yield of its inbred parents” (SCHNELL, 1974).

2. Relative heterosis for grain yield has decreased over the years according to two reports, but increased slightly in a third study. Relative heterosis is defined as “absolute heterosis as percentage of single cross yield” (SCHNELL, 1974).

3. Absolute heterosis for plant size and maturity has decreased to a small degree, in contrast with heterosis for grain yield.

**SUMMARY AND CONCLUSIONS**

Maize grain yields have risen continually in the U.S. since the 1930s, concomitant with changes in crop management and with the utilization and improvement of hybrid maize. Approximately 40 to 50% of the yield gains are owed to changes in management (e.g., use of herbicides, increased amounts of nitrogen fertilizer) and 50 to -60% to continuing genetic improvements in maize hybrids released during the past seven decades.
Studies indicate continuing changes in hybrid genotype as measured with pedigree records and molecular markers, an indication that genetic diversity in time (also called temporal genetic diversity) has been involved in the creation of genetic improvements during the past seven decades of hybrid breeding.

Genetic improvements can be arbitrarily classified as (a) those that promote greater efficiency in grain production, and (b) those that provide increased tolerance to abiotic and biotic stresses. Examples of improvements in efficiency are: smaller tassels, more upright leaves, fewer tillers, and lower grain protein percentage. Examples of improvements in stress tolerance are improved staygreen, increased tolerance to heat and drought, increased tolerance to excessively cool and wet growing conditions, reduced barrenness under abiotic stress, greater tolerance of higher plant density (high density accentuates abiotic stress), and less root and stalk lodging.

Absolute heterosis has increased over the years, primarily when hybrids are subjected to abiotic stress, but has not been the major source of genetic gains in yield.

Yield potential per plant has not increased over the years. Increased yielding ability of the newer hybrids is owed primarily to increases in stress tolerance, that in turn provide tolerance of higher plant densities. Compared with the older hybrids, today’s hybrids produce approximately the same amount of grain per plant, but on considerably more plants per unit area.

**REFERENCES**


