

Heterosis Decreasing in Hybrids: Yield Test Inbreds

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ABSTRACT

Yield testing finished inbreds to replace preliminary single-cross corn (*Zea mays* L.) yield tests will increase rate of commercial hybrid yield gains. Studies have shown that heterosis decreased 25%/50 yr, 10%/60 yr, and 35%/100 yr. Natural selection and artificial selection by plant breeders for adaptedness have increased parental inbred and hybrid seed yields, whereas percentage heterosis decreased. Four studies have shown inbred yields increased 1.9 to 3.5 times faster than heterosis yields. Pioneer Hi-Bred generates 700 new inbreds tested in 6000 single-cross hybrids at 15 to 20 locations annually. Predicted, untested, newer hybrids are then made and tested extensively with commercial hybrids. Parental inbred yield testing is the next to last of several steps in hybrid development. Commercial hybrid development costs have increased logarithmically, whereas performance has increased linearly. Replacing preliminary testcross trials with finished-inbred yield trials is more efficient. About 12,000 new finished inbreds can be evaluated annually with no testers and at least 50% fewer locations per inbred with the same testing effort as 700 new inbreds with testers. A calendar year per breeding cycle and annual production costs for 6000 hybrids will be saved. Corn yield trials detect stress susceptibility, which is more apparent in inbreds than in hybrids. Evaluation of more new inbreds will be conducive to increased genetic diversity that produces higher-yielding hybrids.

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Abbreviations: PHBI, Pioneer Hi-Bred International; PVP, Plant Variety Protection.

CORN (*Zea mays* L.) production in the United States was 53 million Mg annually and corn yield averaged 1518 kg ha⁻¹ in the 1930s, when corn hybrids were first commercially grown. Corn production grew to 76 million Mg annually in the 1950s, to 150 million Mg annually in the 1970s, and to 219 million Mg in the 1990s (USDA National Agricultural Statistics Service, 2007). In 2001 corn became the highest tonnage cereal crop worldwide: 557.6 million Mg of corn, 542.4 million Mg of paddy rice (*Oryza sativa* L.), and 535.6 million Mg of wheat (*Triticum aestivum* L.) (FAO, 2002). In 2004 the U.S. record corn yield was 10,059 kg ha⁻¹, and in 2007 the U.S. record corn production was 332.7 million Mg (USDA National Agricultural Statistics Service, 2007).

World corn production provides feed, food, and fuel for more than 6,000 million humans. World population continues to increase in the face of higher food costs, less arable land, water scarcity, and the threat of global warming with rising temperatures and carbon dioxide levels. Nobel Laureate Dr. Norman Borlaug (2007) predicted the demand for cereals worldwide will probably grow by 50% during the next 20 yr. Monsanto Co. (St. Louis, MO) has recently announced a “sustainable yield initiative,” which includes the goal of doubling corn yields by the year 2030 (Lohuis et al. (2008), www.monsanto.com [verified 31 July 2009]). Studies by international organizations such as the United Nations, the World Bank, and other global experts emphasize unprecedented growth in global demand for cereals.

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We can expect increasing yields of U.S. hybrid corn, but corn breeders need to accelerate the rate of development of higher-yielding, finished corn inbreds to increase the occurrence of higher-yielding corn hybrids. Yield testing finished inbreds to replace preliminary balanced single-cross yield tests to evaluate inbreds will increase the yield gains of commercial hybrids.

More finished inbreds are conducive to more genetic diversity that increases percentage heterosis.

MATERIALS AND METHODS

We examined four, independent, comprehensive, heterosis studies comparing parental finished inbreds to their hybrids across 29-, 53-, 60-, and 100-yr time periods. Schnell (1974) summarized 17 corn heterosis experiments grown in the U.S. Corn Belt from 1916 to 1969. In each experiment, a number of finished inbred lines were evaluated together with a complete or a balanced set of single-cross hybrids made from those lines. We simplified Schnell's intricate figure to the four basic regressions across time for each of the three studies; we regressed the means for inbred or cultivar yields, heterosis yields, and hybrid yields along with percentage heterosis across years of time periods.

Duvick (1984, 1999) and Duvick et al. (2004) summarized data on Pioneer Hi-Bred International (PHBI; Johnston, IA) commercial hybrids introduced in central Iowa across five decades. The tests included 47 commercial hybrids and their inbred parents together in bordered plots at three plant densities in a total of nine locations in 3 yr (~5000 plots). He also summarized data on six sets of 10 single-cross hybrids, each set made from the five most widely used unrelated inbreds in PHBI for central Iowa in each of the six decades. These

60 hybrids and their parent inbreds were tested together in bordered plots in three plant densities at two locations for 2 yr (~1500 plots). We averaged Duvick's two estimates by decades for the first five decades and used only the single-cross data for the sixth decade.

Campbell et al. (2008) summarized data on five modern and five obsolete cotton (*Gossypium hirsutum* L.) cultivars test crossed on a modern cotton cultivar. In 2005 10 hybrids and 11 cultivars, including the tester, were grown together in four replication, randomized block field trials in Alabama, North Carolina, and South Carolina using two-row entry plots 10.7 m long. Mechanically harvested cotton yield minus lint yield calculated from a 25 or 50 boll ginned sample equals seed yield per plot. Cotton breeders and farmers are most interested in cotton fiber (lint) yield and not as much in seed yield (T. Campbell, personal communication 2009).

Mikel (2008) studied agronomic data, including parental finished inbred and hybrid yields in U.S. Plant Variety Protection (PVP) Act and utility-patent records for 846 proprietary corn inbreds and their hybrids for the 1976 through 2005 era. Heterosis data were not calculated.

RESULTS

Schnell (1974) stated that only a modest increase in heterosis yields occurred compared with a large simultaneous increase in inbred yields across time, which represented the average nonheterotic part of the yields of corresponding hybrids. Percentage heterosis decreased from about 75% in 1916 to about 50% 53 yr later. Parental inbred yields increased at $b = 168.9 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ($r^2 = 0.65$), heterosis yields increased at $48.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ($r^2 = 0.08$), hybrid yields increased at

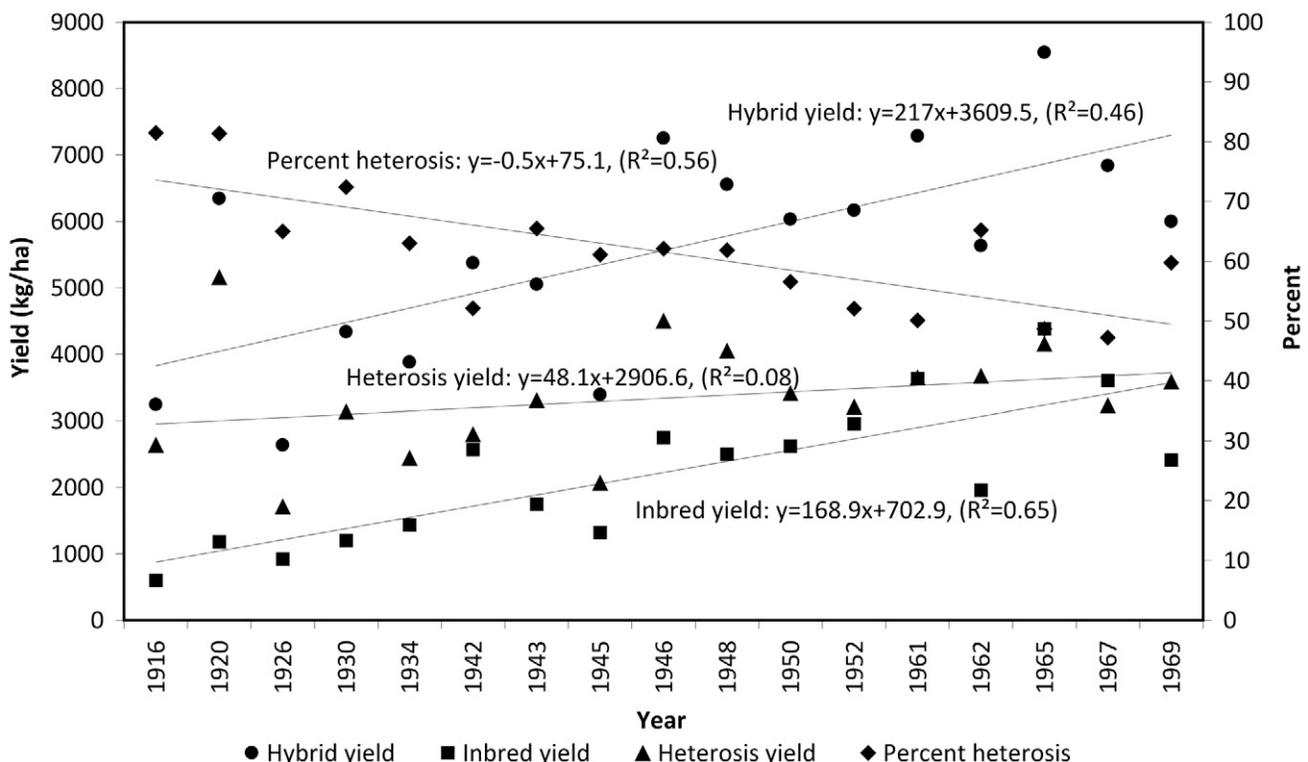


Figure 1. Percentage heterosis, heterosis yield, experimental hybrids yield, and inbreds yield of corn regressed on year of experimentation (Schnell, 1974).

$b = 217 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ($r^2 = 0.46$), and percentage heterosis decreased at $-0.5\% \text{ yr}^{-1}$ ($r^2 = 0.56$) (Fig. 1).

According to Duvick (1999), yields of finished inbreds and their hybrids increased continuously since the 1930s. Heterosis yield increased in all experiments. These yield increases were genetic because entries from all decades were tested together in the same environments. Percentage heterosis decreased in more recent decades. Yield gains in the hybrids always were accompanied by improvements in tolerance to stresses; the improvements occurred in parental inbreds as well as in their hybrid progeny. Percentage heterosis will probably continue to decrease in years to come because of inbred yield improvement. Parental inbred yields increased at $b = 48.3 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ($r^2 = 0.98$), heterosis yield increased at $25.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ($r^2 = 0.88$), hybrid yields increased at $b = 74.0 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ($r^2 = 0.97$), and percentage heterosis decreased at $-0.2\% \text{ yr}^{-1}$ ($r^2 = 0.94$) (Fig. 2). Inbred yields increased almost twice as fast as heterosis yields; thus, percentage heterosis decreased across time.

Campbell et al. (2008) noted that significant differences were detected between groups of modern and obsolete cotton cultivars for seed yield; obsolete cultivars produced larger percentage heterosis for seed yield. Parental cultivar seed yields increased at $b = 12.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ($r^2 = 0.86$), heterosis yield decreased at $-6.3 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ($r^2 = 0.66$), hybrid yields increased at $b = 6.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ($r^2 = 0.75$), and percentage heterosis decreased at $-3.4\% \text{ yr}^{-1}$ ($r^2 = 0.77$) (Fig. 3). Cotton breeders effectively

increased cotton cultivar seed yields. We would expect natural selection to help increase cultivar yields. These seed yield increases were genetic because all entries were tested together in the same environments.

According to Mikel (2008), corn inbred yields increased 6% and hybrid yields increased 2.2% per breeding cycle from 1976 through 2005 based on surveyed U.S. utility patent and PVP registrations of 846 popular commercial inbreds and their hybrids. A positive correlation ($r = 0.36^{**}$) between inbred and hybrid yield existed.

Across these four investigations, beginning in 1905 and ending in 2005, inbred yields increased from 1.9 to 3.5 times faster than heterosis yields across time. Percentage heterosis decreased in all four investigations across time.

DISCUSSION

The first corn inbreds were very low yielding because of deleterious recessive genes and poor adaptedness. Testers were needed to predict their usefulness in hybrids. Open-pollinated varieties were first used as testers (Hayes and Johnson, 1939), and then diallel single-cross sets were used to predict double-cross hybrid performance (Jenkins, 1934). When single-cross hybrids became popular in the mid-1960s, balanced single-cross sets were used to evaluate an inbreds average performance and to determine its particular heterotic patterns (Troyer, 1965a,b).

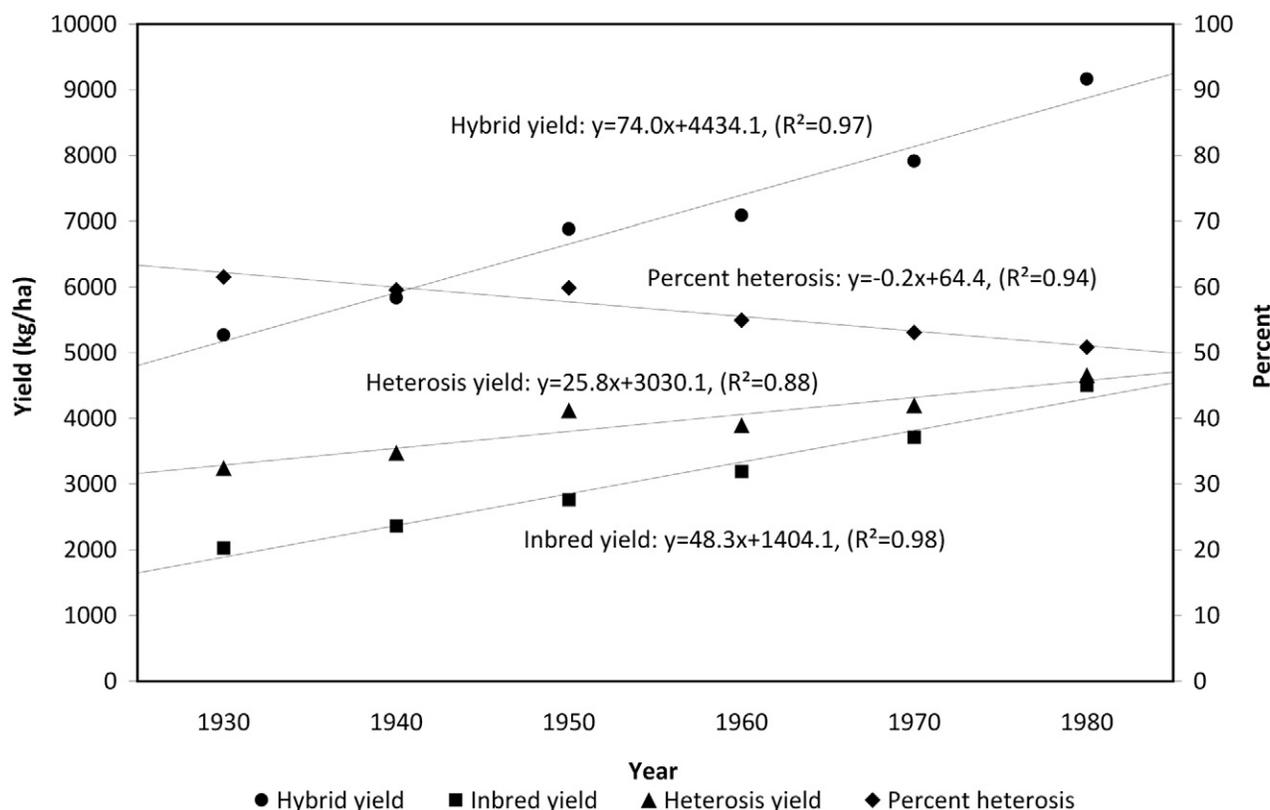


Figure 2. Percentage heterosis, heterosis yield, commercial hybrids yield, and inbreds yield of corn regressed on decade of hybrid popularity (Duvick, 1999; Troyer, 2006),

Development of Inbreds and Hybrids at PHBI

Duvick's (1999) results provide the most pertinent data on finished inbred yields predicting hybrid corn yields because we are primarily interested in commercial corn hybrid yields. For this reason, we provide a brief description of PHBI methods (Smith, 1997; Smith et al., 1999). Similar methods are used by other seed corn companies.

According to Smith (1997), PHBI annually generated more than 700 newly coded, finished inbreds crossed with currently elite inbreds to generate 6000 single-cross hybrids grown in wide-area tests at 15 to 20 locations annually in part to predict newer, untested, potential, single-cross, commercial hybrids. It is a multistep, cut-and-try process. Untested, predicted hybrids are then made and tested extensively along with existing commercial and competitors' hybrids before commercial designation. Smith et al. (1999) emphasized the vagaries of nonadditive gene actions, differing environments, and multiple interactions affecting performance; these vagaries make estimates or predictions for unknowns questionable. Smith (1997) noted that research development costs for commercial corn hybrids have increased almost logarithmically since the 1980s, whereas performance has increased linearly at about 90 kg ha⁻¹ yr⁻¹ during this same period. Smith (1997) identified the need for a more efficient inbred and hybrid evaluation and graduation scheme.

Pioneer Hi-Bred International breeders had freedom to modify breeding methods, but they were pragmatic in staying close to what had worked well in the past. They realized higher yielding inbreds were desirable; they usually advanced inbreeding rows that produced larger piles of corn at the end of their rows. During the 60-yr period from the 1930s to 1980s, the informal consensus of opinion was that the early-testing corn breeding philosophy (Jenkins, 1935) was too expensive for a commercial company where research budgets were sensitive to sales volume. Several PHBI U.S. Corn Belt stations have completed several cycles of cumulative selection (Richey, 1945); PHBI breeders have developed 44,000 named (coded) inbreds (G. Graham, personal communication 2008).

Inbred development at PHBI was modified across time. Breeders testcrossed S₇ and S₈ inbreds in the 1950s. Then, many began testcrossing S₄ bulked seed of visually selected S₃ rows in the early 1960s for a faster system using winter programs (Troyer, 2000); inbreds were bulked at S₅ or S₆ (Troyer, 2000). Testcrosses were typically grown at two or more locations before new inbreds were named (coded). The Jenkins (1934) method was used to predict double crosses from diallel single-cross tests. By the mid-1960s, top-crossing was sometimes omitted and the better, stronger inbreds were each crossed to a particular inbred(s) for a potential commercial single-cross hybrid(s) or were testcrossed with four or five inbred testers, on

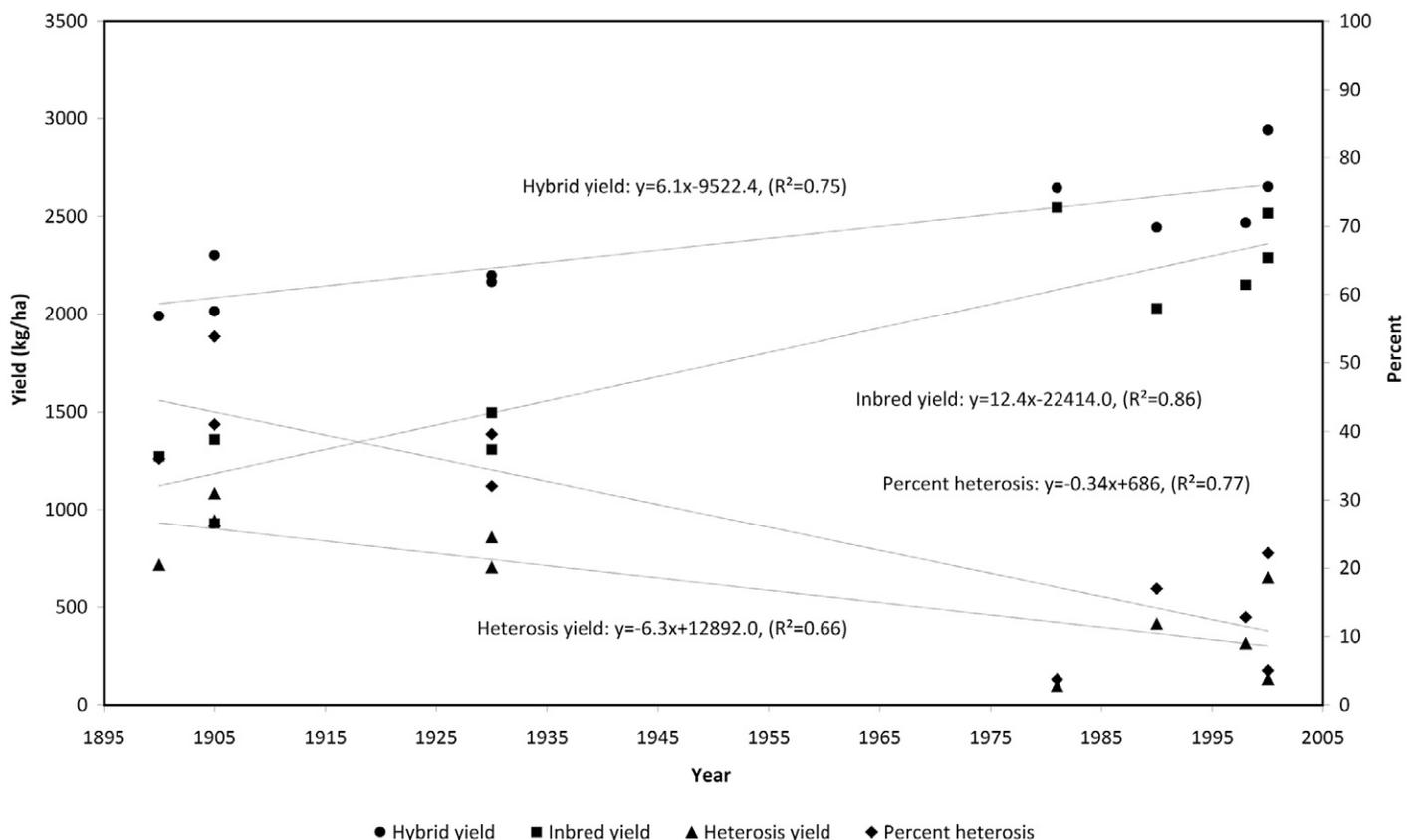


Figure 3. Percentage heterosis, heterosis yield, experimental hybrids yield, and cultivars yield in cotton regressed on year of cultivar introduction (Campbell et al., 2008).

the basis of genetic background, and grown at multiple locations to determine average (general) combining ability and to identify potential commercial hybrids (Troyer, 1965a,b, 1996).

Progress occurred in developing better inbreds and hybrids. Hybrids were typically grown as new hybrids 1 yr, retest hybrids 1 yr, and precommercial hybrids 2 yr before being launched as a commercial hybrid. New parental inbreds were not yield tested until they became parents of precommercial hybrids. Winter breeding programs became available in the mid-1950s with the advent of male sterile and restorer backcross conversions. Computer analyses of yield test plots began in 1957. Perry Collins developed PHBI's first commercial single-cross hybrid, Pioneer 3755, which was launched in 1962. Higher plant densities for yield tests were first used across stations, and combine harvest of most yield test plots first occurred in 1965. Wide-area testing, across multiple research stations, began in 1966 (Troyer, 1996).

Unique hybrid reference numbers became possible with the IBM 360 computer; head-to-head comparisons followed (Bradley et al., 1988). Head-to-head comparisons and wide-area testing effectively reduced provincialism among breeders. Farmers' strip test results were included for commercial hybrid graduation in 1971 (Duvick, 2004). Widely adapted hybrids Pioneer 3780 and Pioneer 3732 were launched in 1972 and 1976, respectively (Troyer, 1996). Data-driven winter breeding nurseries first occurred in the early 1990s. Multiple factors included larger farm operators with larger equipment, earlier planting causing earlier harvest, earlier flowering and faster drying corn hybrids causing less grain damage in field shelling, and an increase in the cost of artificially drying grain. Briefly stated, field shelling caused earlier harvest, which shortened breeding cycle time. Yield test results helped plan the following winter nurseries.

Pioneer Hi-Bred International gained market share during the 1930s through the 1980s, except for a short dip due to dropped ears caused by European corn borer (*Ostrinia nubilalis* Hübner) in the hot, windy 1964 and 1965 fall seasons. In 1989 at the end of the 1930s to 1980s period, Pioneer brand seed corn held market share of about 34% in North America; PHBI's closest competitor held approximately 9% (Pioneer Hi-Bred Int., 1990).

Heterosis

Heterosis is poorly understood. Despite extensive study, its genetic basis remains unresolved (Troyer, 2006; Hallauer, 2007). Heterosis yield equals hybrid yield minus inbred parents' average (midparent) yield, and percentage heterosis equals heterosis yield divided by inbred parents' average (midparent) yield. Percentage heterosis decreases as the inbred parent yield increases for the same hybrid yield. Inbred yields have been increasing ever since hybrid corn was first developed. East and Jones (1919) stated that

heterosis was most noticeable as an increase in plant size; for example, in a large number of crosses, the increase in plant height in hybrids averaged 27%. The main effect of heterosis, however, is an additional production of seed. East and Jones (1919) reported crosses that had 180% increases in yield of grain over their inbred parents. They reported a general positive correlation between the yield of the better inbred parent strains and the yield of their hybrids. Figure 2 illustrates heterosis yield and parent inbred yield in the 1980s about equal with parent inbred yield increasing about twice as fast.

Heterosis in corn is a good thing, but like all good things, it can be overdone. Too much heterosis information in corn is like too much diversification in financial investment—it becomes redundant. Evaluating new, finished inbreds in balanced sets of single crosses (Troyer, 1965a, 1965b) presently provides relatively little useful heterosis information at a very high cost (Smith, 1997).

Inbred Yields

As already noted, inbred yields have been increasing ever since hybrid corn was first developed. The first-generation inbreds, developed from open-pollinated cultivars, barely survived. They were very poor for agronomic traits (Baker, 1984). Corn breeders saw these faults as opportunities to improve inbreds. Troyer (2006) reported 122% yield gain of PHBI inbreds across 60 yr, which testifies to their plant breeders' prowess after starting from a very low base. East and Jones (1919) reported a general positive correlation between the yield of the better inbred parent strains and the yield of their hybrids. Richey and Mayer (1925) and Richey (1945) reported that higher-yielding inbreds consistently tended to produce higher-yielding hybrids.

Many inbreds were developed by recurrent, pedigree selection with late testing (Hayes and Johnson, 1939). Richey (1945) named this method *cumulative selection* and predicted the forthcoming increase in inbred yields. He titled his paper "Isolating Better Foundation Inbreds for Use in Corn Hybrids." Richey's conclusions were based on widespread use of the pedigree method and recycling of elite inbreds across the U.S. Corn Belt (Hallauer and Miranda, 1988; Troyer, 2006). Mikel and Dudley's (2006) figures of lineage illustrate the extensive recycling of elite inbreds. Richey (1945, 1950) advocated selection against gross, deleterious, recessive gene effects in early generations, followed by selection for selfed progeny performance in later generations or in later cycles of inbred development; he advocated the late-testing corn breeding philosophy.

Clearly, significantly higher yielding inbreds have been developed. The yield gains of parental inbreds and their hybrids for the first 60 yr of hybrid corn development are mostly due to genetic improvements for overcoming biotic and abiotic stresses, resulting in better adaptedness to improved cultural practices and to their

natural environment (Duvick 1999). Our thesis is that improved inbreds currently used by the industry are much better adapted and have fewer deleterious recessive genes with less effect; therefore, we can dispense with testers and measure inbred performance per se to estimate its worth in hybrids (Troyer, 2006). The genetic justification for yield testing inbreds to estimate general combining ability is that cumulative selection has decreased the number of deleterious recessive genes in inbreds, thus increasing the association between finished inbred and hybrid yield. Duvick's (1999) results call for more attention to inbred line development and less expenditure on elaborate new inbred testing schemes. Good hybrids are not found; they are made from good inbreds (Troyer, 1996, 2000).

Presently, inbred yields are increasing across time even though hybrids graduate twice from new to retest and from retest to precommercial before inbreds are yield tested. Inbred yield is following hybrid yield upward at present—the cart is before the horse. Yield testing and graduating higher-yielding inbreds before making new hybrids will properly correct the relationship to higher inbred yield pulling hybrid yield upward. We expect selecting higher-yielding inbreds to increase the occurrence of higher-yielding hybrids. How could it not?

Increasing Evaluation and Graduation Efficiency

Evaluating inbreds with multiple testers is a highly cumbersome and highly expensive way of increasing the adaptedness of inbred lines, which widens their hybrid's adaptation. The only justification for all this effort with testers is to find partners causing higher heterosis when in fact we are finding lower heterosis in commercial hybrids across time. This is inefficient. Determining heterotic pattern is no longer justification for multiple testers because virtually all U.S. Corn Belt hybrids are now Stiff Stalk by non-Stiff Stalk inbreds; choosing the right pattern is obvious. Plant breeders should more directly measure and improve the adaptedness of inbred parents based on inbred yield. Of course, the genotype of the hybrid is determined completely by the genotypes of its parental inbreds.

Replacing yield trials of preliminary testcrosses with yield trials of new inbreds will increase efficiency. About 12,000 new inbreds can be evaluated in yield trials with about the same effort as 700 inbreds with testers (Table 1). The breeding cycle can be shortened a calendar year, and production costs for 6000 hybrids can be saved annually. This assumes no testers and at least 50% fewer test locations necessary for inbreds to experience abiotic and biotic stresses than hybrids. This approximates a similar amount of testing effort to Smith's (1997) method for 700 inbreds. More rigorous yield testing of inbreds with combine harvesting and multiple, stress locations may increase the correlation between inbred and hybrid yields across time

because of natural and artificial selection for more additive, dominance, and epistatic gene effects.

Inbred yield and other agronomic traits will replace preliminary inbred general combining ability records. Inbred yield testing will better select for stress tolerance because inbreds are more susceptible to stress than their hybrids (Darwin, 1868, 1875; Troyer, 1993, 2006; Duvick, 1999, 2005). An important benefit of inbred yield testing will be that the breeder learns more about plant traits affecting production of hybrids. Inbred yield testing will speed up genetic progress for higher yields. Many more genetic backgrounds will be evaluated when the process is easier and less expensive. It is ironic that eliminating heterosis from the preliminary evaluation of inbreds will result in more genetic diversity that increases heterosis yield in the final hybrids. We suggest testing bulked, selfed seed from individual, uniform, S_5 or S_6 inbred ear rows in different experiments for different inbred families, at multiple locations and years.

These suggestions are a major departure from current thinking and practice, but we offer them to stimulate thinking and discussion to increase hybrid corn yields. The common response to advocating inbred yield testing is that some very poor yielding inbreds have shown much heterosis. The inbred evaluation system we have used in the past not only allows low-yielding inbreds to exist, but it also encourages it with higher heterosis. We need a better system, as Smith (1997) suggested. All concerned will benefit from higher-yielding inbreds. We hope PHBI data for commercial hybrids and parent inbreds in central Iowa for the 1980s, 1990s, and 2000s will be published. We invite other plant breeders with access to large data sets of inbred and hybrid yields to consider the conclusions we state, to consider the suggestion and implications of yield testing finished inbreds earlier in their graduation scheme, and to contribute to the discussion. Increasing the rate of gain in yields of cereals is essential to future world food supply.

CONCLUSIONS

Percentage heterosis decreased significantly across time in three independent studies because parental inbred yields increased from 1.9 to 3.5 times faster than heterosis yields (Schnell, 1974; Duvick, 1999; Campbell et al., 2008). Higher-yielding parental inbreds and hybrids have more tolerance to the abiotic and biotic stresses they frequently encounter (Duvick, 1999; Troyer, 2006). Natural selection and artificial selection by plant breeders for adaptedness over time have increased parental inbred and hybrid seed yields, while percentage heterosis decreased over time (Schnell, 1974; Duvick, 1999; Troyer, 2003, 2006; Campbell et al., 2008; Mikel, 2008).

We need a more efficient evaluation and graduation scheme for commercial corn hybrids; inbred yield tests may be the answer. Inbreds are more susceptible to stresses

than their hybrids (Darwin, 1868, 1875). More inbreds can be evaluated for yield as inbreds than in balanced single cross sets by an order of magnitude equal to the number of testers times at least two. Evaluation of more inbreds would be conducive to more genetic diversity producing higher-yielding (more heterosis yield) corn hybrids. We suggest testing bulked, selfed seed from individual, uniform, S_5 or S_6 inbred ear rows in different experiments for different inbred families, at multiple locations and years.

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Table 1. Preliminary inbred evaluation in balanced single crosses (Smith 1997) compared with evaluating inbreds per se.

Step	Balanced Sets	Inbreds per se
1	700 inbreds	12,000 inbreds
2	Make 6,000 single crosses	12,000 inbreds at 10 locations = 120,000 plots
3	6,000 single crosses at 20 locations = 120,000 plots	Make new hybrids to compare with commercials Start new cycle
4	Make new hybrids to compare with commercials Start new cycle	

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