Heterosis Decreasing in Hybrids--Yield Test Inbreds

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U.S. corn production 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/NASS 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.) (UN/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/NASS 2007).

World corn supply provides feed, food, and fuel. 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% over the next 20 years. Monsanto Co. 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). Study upon study by international organizations such as the United Nations, the World Bank, and other experts paint a picture of unprecedented growth in global demand for cereals.

We can count on increasing yield levels of U.S. hybrid corn to help, but corn breeders need to accelerate the rate of development of higher yielding inbreds to increase the occurrence of hybrid corn yield increases. We believe yield testing inbreds to replace preliminary single cross yield tests will increase yield gains of commercial hybrids.

MATERIALS AND METHODS

In this paper we examine comprehensive heterosis studies comparing parents to their hybrids over long periods of time: Schnell (1974) summarized 17 corn heterosis experiments grown in the U.S. Corn Belt from 1916 to 1969. In each experiment a number of inbred lines were evaluated together with a complete or a balanced set of single cross hybrids made from those lines. Duvick (1984, 1999; Duvick et al 2004) summarized data on PHBI (Pioneer Hi-Bred Intl.) commercial hybrids introduced in central Iowa over 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 three years (ca 2500 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 two years (ca 960 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 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 (252 plots) using two row entry plots.

We simplified Schnell's intricate figure to use for each of the three studies: We regressed the means for inbred yields, heterosis yields, and hybrid yields along with heterosis percent over periods of time.

RESULTS

Schnell (1974) stated only a modest increase in heterosis yields occurred as compared to a large simultaneous increase in inbred yields, which indeed represent the average non-heterotic part of the yields of corresponding hybrids. Heterosis percent decreased from about 75% at the beginning to about 50% at the end of about 50 years. Figure 1 shows parental inbred yields increasing at b = 168.9 kg ha^{-1} yr^{-1} with an r^2 = 0.65, heterosis yields increasing at 48.1 kg ha^{-1} yr^{-1} with an r^2 = 0.08, hybrid yields increasing at b = 217 kg ha^{-1} yr^{-1} with an r^2 = 0.46, and heterosis percent decreasing at -0.5 % yr^{-1} with an r^2 = 0.56.

Duvick (1999) stated yields of inbreds and their hybrids have risen continuously since the 1930s. Heterosis yield rose in all experiments. These yield increases were definitely genetic because all decades entries were tested together in the same environments. Heterosis percent declined in more recent decades. Yield gains in the hybrids always were accompanied by improvements for tolerance to stresses; the improvements occurred in parental inbreds as well as in their hybrid progeny. *Heterosis percent will probably continue to decrease in years to come because of inbred yield improvement.* Figure 2 shows parental inbred yields increasing at b = 48.3 kg ha^{-1} yr^{-1} with an r^2 = 0.98, heterosis yield increasing at 25.8 kg ha^{-1} yr^{-1} with an r^2 = 0.88, hybrid yields increasing at b = 74.0 kg ha^{-1} yr^{-1} with an r^2 = 0.97, and heterosis percent decreasing at -0.2% yr^{-1} with an r^2 = 0.94. Inbred yields increased almost twice as fast as heterosis yields; thus heterosis percent decreased over time.

Campbell et al. (2008) stated significant differences were detected between groups of modern and obsolete cultivars for seed cotton yield; obsolete cultivars produced larger heterosis percent values for seed yield. Figure 3 shows parental cultivar yields increasing at b = 12.4 kg ha^{-1} yr^{-1} with an r^2 = 0.86, heterosis yield decreasing at -6.3 kg ha^{-1} yr^{-1} with an r^2 = 0.66, hybrid yields increasing at b = 6.1 kg ha^{-1} yr^{-1} with an r^2 = 0.75, and heterosis percent decreasing at -3.4% yr^{-1} with an r^2 = 0.77. Cotton breeders effectively increased cotton cultivar seed yields. These yield increases were definitely genetic because all entries were tested together in the same environments.

DISCUSSION

Development of Inbreds and Hybrids at PHBI

Duvick's (1999) results provide the most pertinent data on inbred yields affecting hybrid corn 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.

Smith (1997) stated PHBI annually generates more than 700 newly coded 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 multi-step, cut-and-try process. Untested, predicted hybrids must then be made and tested extensively with existing commercial and competitor's hybrids before commercial designation. Smith et al (1999) emphasized the vagaries of non-additive gene actions, differing environments, and multiple interactions affecting performance; these vagaries make estimates or predictions for unknowns questionable. Smith (1997) stated that research development costs for commercial maize 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 identified the need for a more efficient inbred and hybrid evaluation and graduation scheme.

PHBI breeders had freedom to modify breeding methods, but they were pragmatic in staying close to what had worked in the past. They realized higher yielding inbreds were desirable; they advanced inbreeding rows with larger piles of corn at the end of their rows. During this 60 year period from the 1930s to 1980s, the informal consensus of opinion was that the early testing corn breeding method (Jenkins 1935) was too expensive for a commercial company where research budgets are 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 inbreds (G. Graham pers. comm. 2008).

PHBI inbred development was modified over 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; 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, based on genetic background, and grown at multiple locations to determine average (general) combining ability and to identify potential commercial hybrids (Troyer 1965a, Troyer 1965b, 1996).

Progress occurred in developing better hybrids. Hybrids were typically grown as new hybrids one year, retest hybrids one year, and pre-commercial hybrids two years before becoming a commercial hybrid. New inbreds were first yield tested when they became parents of pre-commercial 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 further reduced provincialism among breeders. Farmers' strip test results were included for commercial hybrid graduation in 1971 (Duvick 2004). Widely adapted hybrids Pioneer 3780 and 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 caused less late planting, earlier flowering and faster drying corn hybrids caused less grain damage in field shelling, and cost of artificially drying grain increased. Yield test results helped plan winter nurseries. Briefly stated, field shelling caused earlier harvest, which shortened breeding cycle time.

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

Heterosis

Heterosis is poorly understood. In spite of extensive study, its genetic basis remains unresolved (Troyer 2006, Hallauer 2007). Heterosis yield equals hybrid yield minus inbred parents' average (midparent) yield. Heterosis percent equals heterosis yield divided by hybrid yield. Heterosis percent 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 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 reported crosses that had 180% increases in yield of grain over their inbred parents, which would be 64% heterosis. They reported a general positive correlation between the yield of the better inbred parent strains and the yield of their hybrids. Fig. 2 shows 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 inbreds in balanced sets of single crosses (Troyer 1965a, 1965b) presently provides relatively little useful heterosis information at a very high cost.

Inbred Yields

Again, inbred yields have been increasing ever since hybrid corn was first developed. The first generation inbreds, developed from open-pollinated cultivars, barely survived, 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 over 60 years, 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 the higher yielding hybrids. Many inbreds were developed by recurrent, pedigree-method 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 method. Clearly, better, much higher yielding inbreds have been developed. Mikel (2008) stated inbred yield increased 6% and hybrid yield 2.2% per breeding cycle from 1976 through 2005 based on surveyed U.S. utility patent and PVP registrations. A positive correlation (0.36) between inbred and hybrid yield existed.

The yield gains of parental inbreds and their hybrids for the first 60 years of hybrid corn are mostly due to genetic improvements for overcoming biotic and abiotic stresses causing better adaptedness to improved cultural practices and to their natural environment (Duvick 1999, 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 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 over time even though hybrids graduate twice from new to retest and from retest to pre-commercial before inbreds are yield tested. Inbred yield is following hybrid yield upward at present--the cart is before the horse. Yield testing and graduating inbreds before making new hybrids will properly correct the relationship to higher inbred yield pulling hybrid yield upwards. 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 very cumbersome and expensive way of increasing the adaptedness of inbred lines. The only justification for all this effort with testers is to find partners causing higher heterosis when in fact we're finding lower heterosis in commercial hybrids over 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. Inbred yield testing will speed genetic progress. We suggest testing bulked, selfed seed from individual, uniform, S5 or S6 inbred ear rows with different experiments for different inbred families, at multiple locations and years.

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. The breeding cycle can be shortened a calendar year and production costs for 6000 hybrids can be saved annually. This assumes no testers and 50% fewer test locations necessary for inbreds to experience abiotic and biotic stresses. This approximates a similar amount of testing effort to Smith et al.'s (1999) method for 700 inbreds. More rigorous yield testing of inbreds with combine harvesting and multiple, stressed locations will increase the correlation between inbred and hybrid yields over time because of natural and human selection for more additive, dominant, and epistatic gene action 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 the breeder learning more about plant traits affecting production of hybrids.

We recognize these suggestions are a major departure from current thinking and practice but offer them to stimulate thinking and discussion to increase hybrid corn yields. 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 inbreds early in their graduation scheme, and to contribute to the discussion. Increasing the rate of gain in yields of cereals is essential to the world food supply of the future.

CONCLUSIONS

1. Heterosis is important in corn; heterotic patterns and inbred families are useful. We need a more efficient evaluation and graduation scheme; inbred yield may be the answer.

2. Across these three comprehensive experiments, inbred yields increased about twice as fast as heterosis yields. Adaptedness (seed yield) of inbreds is increasing while heterosis percent is decreasing over time (Schnell 1974, Duvick 1999, Troyer 2003, 2006, Campbell et al. 2008).

3. Higher yielding inbreds and hybrids have more tolerance to the abiotic and biotic stresses they frequently encounter (Duvick 1999, Troyer 2006).

4. Inbreds are more susceptible to stresses than their hybrids (Darwin 1868, 1875).

5. 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 two.

6. Evaluation of more inbreds would be conducive to more genetic diversity and to higher yielding (more heterosis yield) corn hybrids.

7. Three comprehensive studies on two major field crops support the theory that natural selection and human selection by plant breeders for adaptedness over time increases parental and hybrid seed yields while decreasing heterosis percent (Darwin and Wallace 1858, Darwin 1859, Schnell 1974, Duvick 1999, Troyer 2006, and Campbell et al. 2008).

8. We suggest testing bulked, selfed seed from individual, uniform, S5 or S6 inbred ear rows with different experiments for different inbred families, at multiple locations and years.

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TABLE - SCHNELL

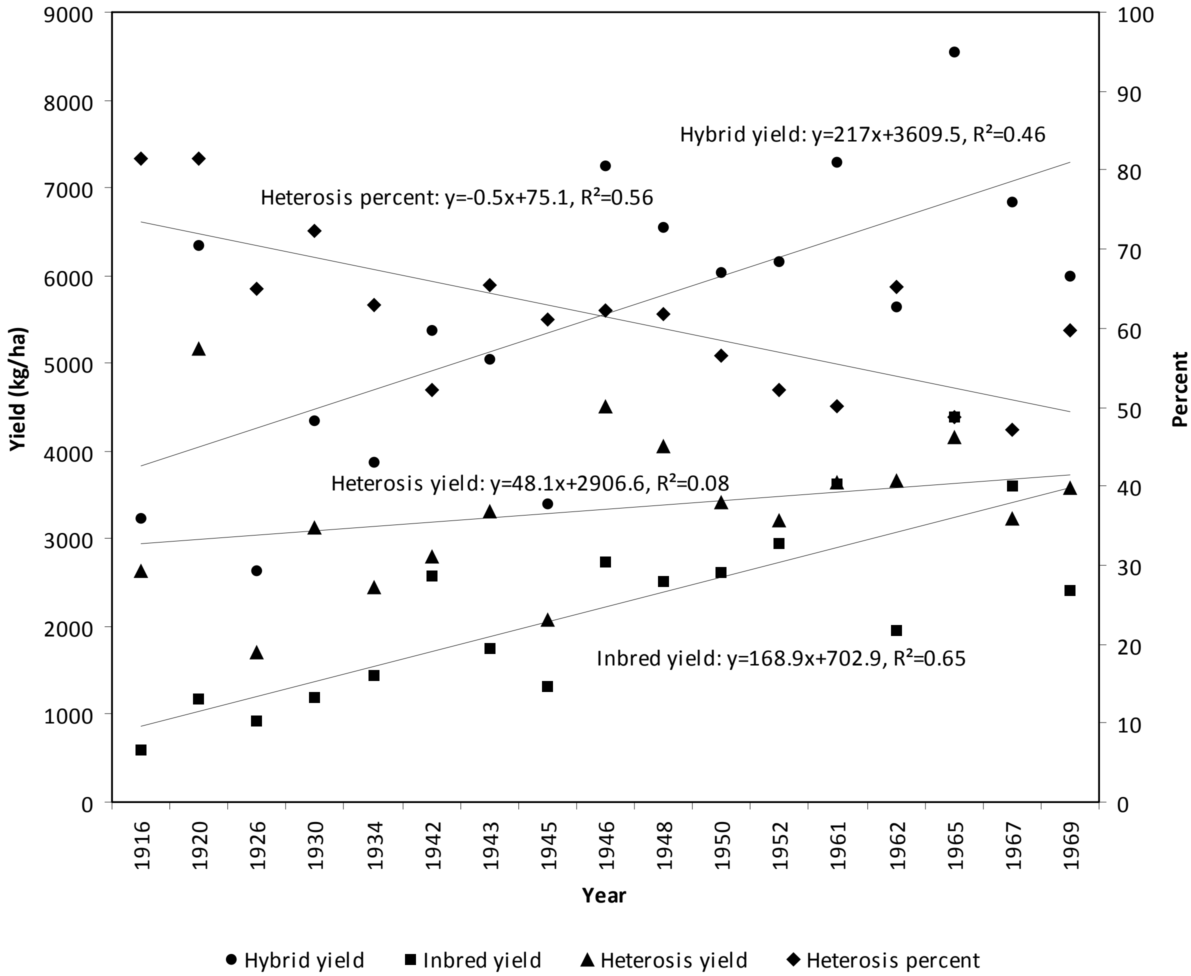

Figure 1. Heterosis percent, heterosis yield, experimental hybrids yield, and inbreds yield of corn regressed on year of experimentation (Schnell 1974).

TABLE - DUVICK

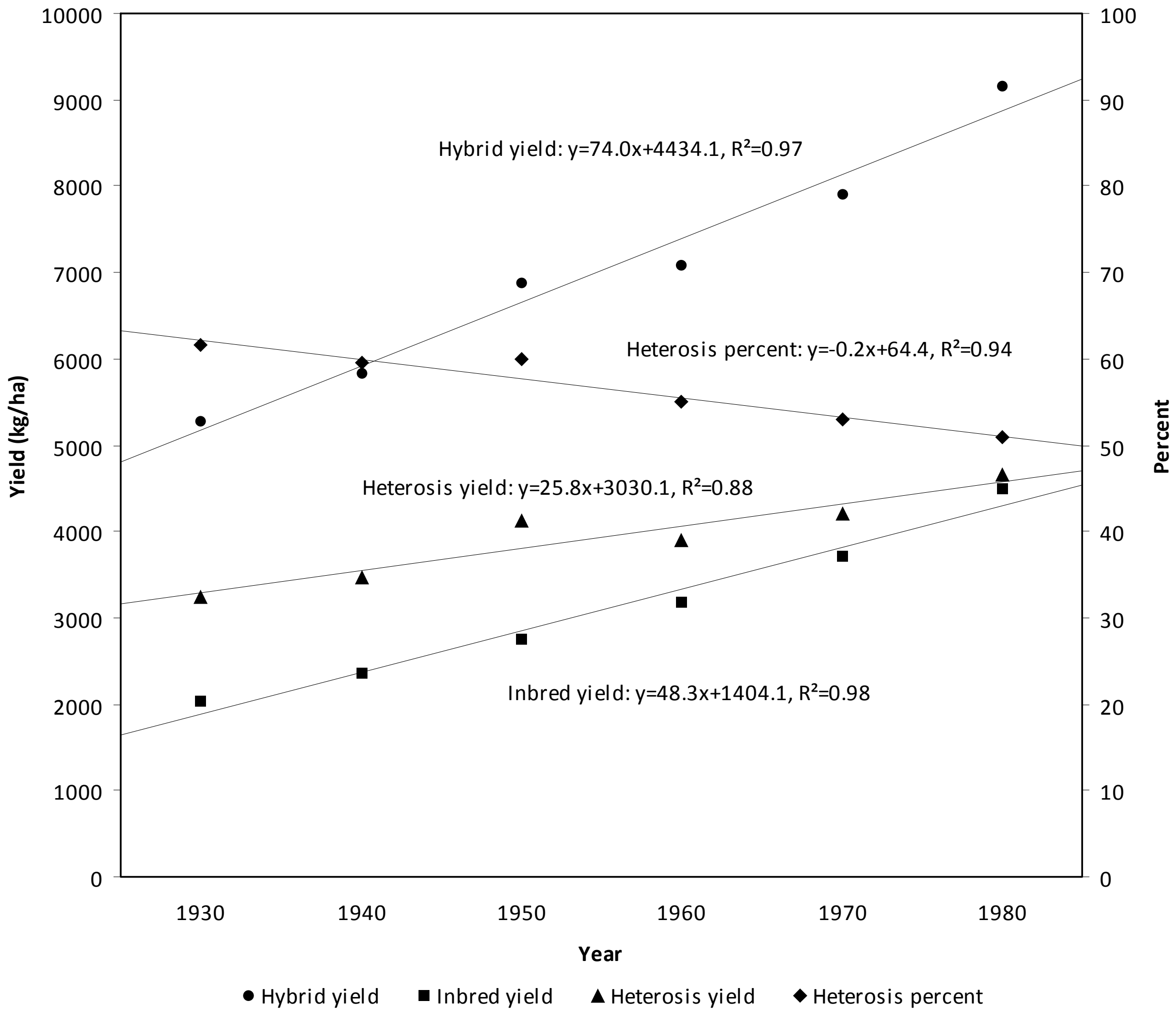

Figure 2. Heterosis percent, heterosis yield, commercial hybrids yield, and inbreds yield of corn regressed on year of hybrid introduction (Duvick 1999, Troyer 2006),

TABLE - CAMPBELL

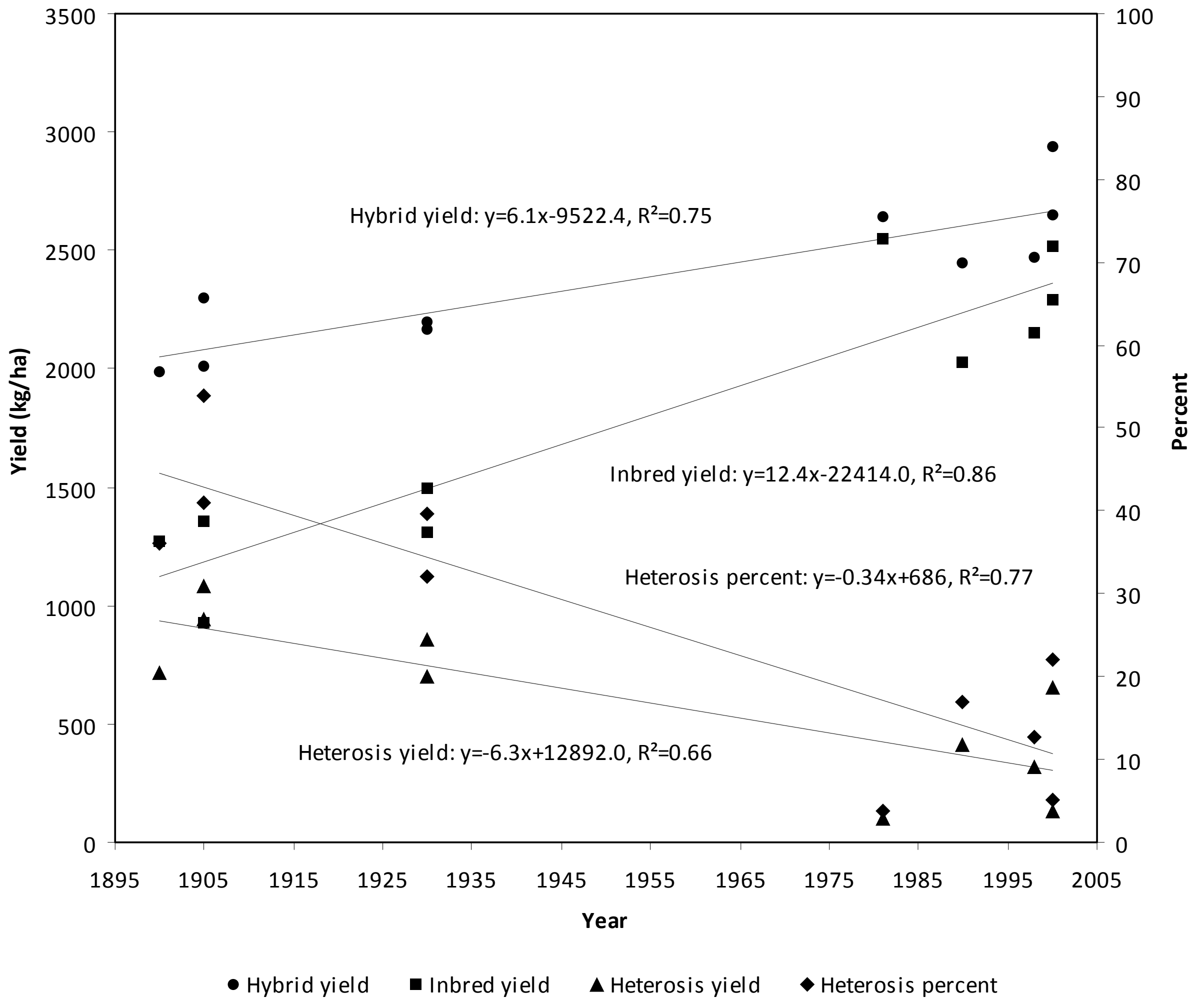

Figure 3. Heterosis percent, heterosis yield, experimental hybrids yield, and cultivars yield in cotton regressed on year of experimentation (Campbell et al. 2008).

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