Adaptedness and Heterosis in Corn and Mule Hybrids

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ABSTRACT

The origin of U.S. Corn Belt corn (*Zea mays* L.), heterotic groups, and heterotic patterns becomes less obvious with more cycles of breeding. Heterosis is poorly understood; simple curiosity cries out for more information. I endeavor to shed light on the effect of adaptedness and heterosis on U.S. Corn Belt corn. I relate pertinent happenings in the phenomenal increase in U.S. corn production. I briefly review the origins of Northern Flint and Southern Dent races of corn and two major, persistent open-pollinated cultivars; and how corn hybridization was preceded and eased by hybrid species of the horse (*Equus* spp.). I discuss heterotic groups and patterns. The objective of U.S. corn breeding has been to adapt a tropical crop to a temperate climate. Adaptedness is important. Open-pollinated cultivars emphasized local adaptation, but some cultivars were more popular, widely grown, and better adapted over a broad geographic region. Hybrid seed corn companies grew larger by selling more widely adapted hybrids that favored germplasm from the more popular, widely grown, better adapted open-pollinated cultivars containing more genes for adaptedness. I examine morphological differences between inbred parents of a widely adapted hybrid. Relatively constant percentage of heterosis of well-adapted hybrids over years is due to seasonal climate affecting hybrids and their parent inbreds in a like manner because of their selection for adaptedness. Adaptedness has been more important than heterosis in the U.S. corn yield and production increases. Adaptedness in analogous heterotic species hybrids of the genus *Equus*, where body size is female dominant, apparently discriminates for body size between mules and hinnies that have virtually identical genotypes—adaptedness determines superiority over and above heterosis.

ON 28 SEPT. 1838, Charles Darwin read Malthus' *Essay on the Principle of Population* and first conceived the concept of natural selection for adaptedness (Encyclopedia Britannica, 1983).

In 2001, corn became the highest tonnage crop worldwide: 557.6 million Mg of maize, 542.4 million Mg of rice (*Oryza sativa* L.) paddy, and 535.6 million Mg of wheat (*Triticum aestivum* L.) (UN/FAO, 2002). United States corn production was 53 million Mg [2 billion (2×10^{-9}) bushels] annually in the 1930s, when corn hybrids were first commercially grown, and yield averaged 1518 kg ha^{-1} (24.2 bushels acre^{-1}). Corn production grew to 76 million Mg (3 billion bushels) annually in the 1950s, to 150 million Mg (6 billion bushels) annually in the 1970s, and to more than 229 million Mg (9 billion bushels) annually for the past 9 yr. The USDA-NASS (2005) estimates 2004 U.S. corn production at a record 299.7 million Mg (11.8 billion bushels) and the average yield is estimated at a record 10 059 kg ha^{-1} (160.4 bushels acre^{-1}) (Fig. 1). At $150 per

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bag for 30 million bags, the annual U.S. seed-corn cost is $4.5 billion. At $2.50 per 25.4 kg (1 bushel) and 299.7 million Mg (11.8 billion bushels), the annual U.S. farm value is $29.5 billion. The relatively high cost of seed corn (~15% of the crop's farm value) is justified by higher yielding, newer hybrids.

I relate pertinent happenings in the phenomenal increases in U.S. corn yield and production. The increases over time are associated with better adaptedness, corn breeding, hybrid corn, mechanical harvest, better soil fertility (particularly more N), single-cross hybrids that are easily identified by the farmer (better hybrid choice), field-shelling harvest (faster feed back for yield), improved cultural practices (particularly higher plant densities), and biotechnology. Heterosis in hybrid corn is well used but poorly understood. I revisit the accepted origin of Corn Belt corn and its heterotic groups and patterns. I address adaptedness due to natural and human selection that caused race and cultivar formation; evolution of heterosis, genetic diversity, and heterotic gene action; corn hybrids including combining ability, heterotic groups and patterns; and mules as the hybrid corn prototype. Major corn events are in chronological order. Mules are an afterthought. I offer the mule as a Rosetta stone providing an easily understood example of natural selection and adaptedness affecting an organism's performance over and above its heterosis. Sections begin with a short description or history of the topic.

Adaptedness

Adaptedness is the degree of suitability of an organism for its environment, developed over time as a result of selection (Allard, 1999). Darwin (1868) states: "Plants may become adapted to climates widely different from their own, from flowering and fruiting either earlier or later in the season… With plants, adaptation to certain soils, the power of resisting frost, the period of flowering and fruiting, the duration of life, the period of shedding the leaves or of retaining them throughout the winter, the proportion and nature of certain chemical compounds in the tissues or seeds, all vary… New races and new species become adapted to widely different climates by variation, aided by habit [crop husbandry], and regulated by natural selection… When the new breed [cultivar] has spread widely, it gives rise to new strains and sub breeds. And the best of these succeed and spread, supplanting other and older breeds and so always onward in the march of improvement." Williams emphasized function to some proximate end as a condition for biological adaptation (Williams 1966, Zimmer 2004).

Natural Selection

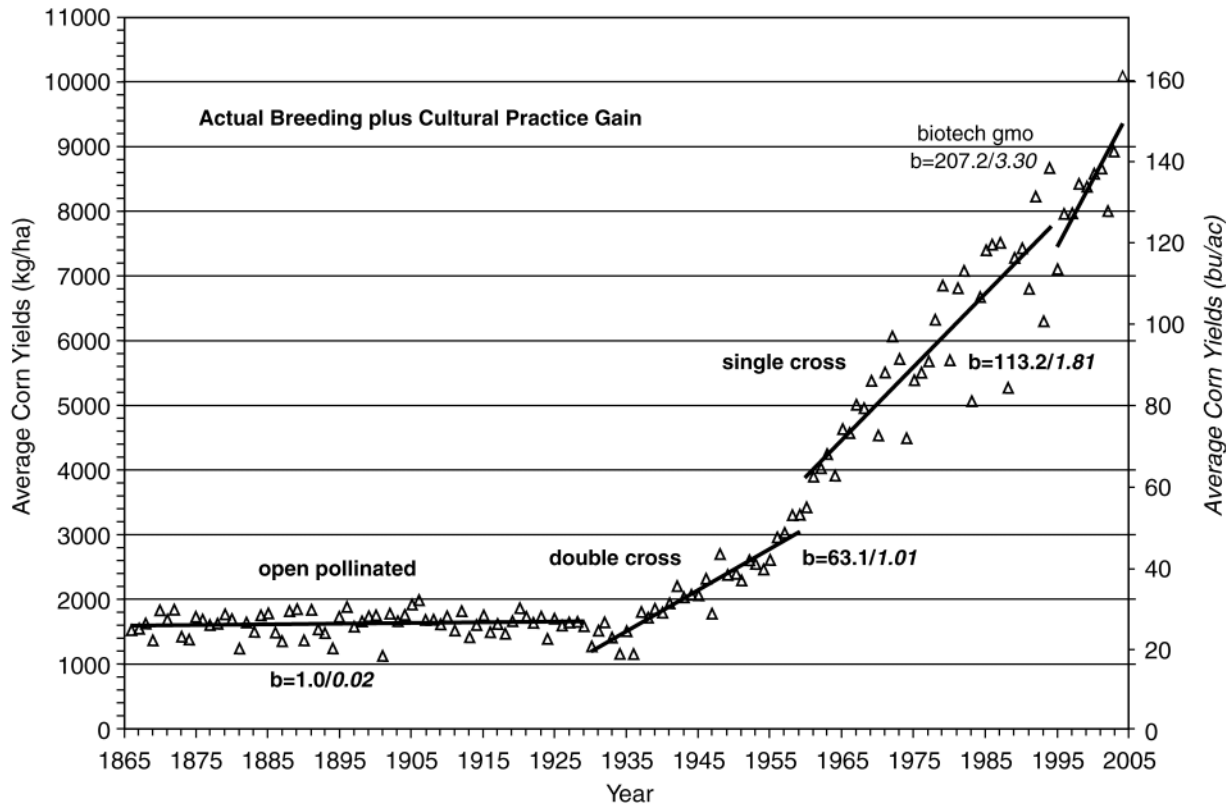Natural selection is sometimes called survival of the fittest. Differential reproduction and survival under

Fig. 1. Average U.S. corn yields and kinds of corn, Civil War to 2004. "b" values (regressions kg bu^{-1}) indicate production gain per unit area per year (USDA-NASS, 2005).

different conditions of life (environment plus cultural practices) is the key. Sheppard (1969) states: "Both Charles Darwin and A.R. Wallace independently put forward the view that species are not individually created and unchanging, but that each could give rise gradually to new species during the course of time. That species are not immutable but can change, or *evolve* as we would now say, was not a new view. However, the point which was new (it had been put forward before in a tentative way but with little detailed argument and evidence to back it) was the hypothesis that natural selection is the essential agent directing and controlling such change."

Darwin (1856–1858) compares Nature's selection with man's selection. He says in part: "It cannot be doubted than man can do and has done much in the modification of animals and plants by the artificial selection of variations. But he labors under great disadvantages; he selects only by the eye and acts therefore on external characters alone… Far from allowing each being to struggle for life; he protects each to the utmost of his power, both during youth and times of dearth [famine] and from all enemies. Instead of selecting steadily from generation to generation, he only occasionally selects and his judgment is often bad or capricious. He and his successors never go on selecting for the same precise object for thousands of generations… See how differently Nature acts: She cares not for mere external appearance; she may be said to scrutinize with a severe eye, every nerve, vessel, and muscle; every habit, in-

stinct, shade of constitution—the whole machinery of the organization… Seeing what man has done in a few thousand years, I have sometimes wondered that Nature, considering the perfection of her means, has not worked quicker, than geology teaches us to believe she has, in the modification of organic beings."

Simmonds (1979) states: "In the evolution of crop plants, we can usually distinguish between natural and human selection. The former is selection inherent in the cultivation of a genetically heterogeneous population at a particular place and time. The latter is the result of conscious decision by the farmer, or plant breeder, to keep the progeny of this or that parent in preference to others. In either case, there will (tend to) be evolutionary change in the form of improved adaptation, that is, enhanced reproductive fitness in the joint circumstances of cultivation and the breeder's desires. The relative importance of natural and human selection has surely changed over the millennia, in favor of the latter but that there was some conscious selection in the earliest phases and that natural selection in the modern plant breeder's plots is still significant seem equally certain." Simmonds lists the following examples of predominantly natural selection: Altered photoperiod and vernalization requirements associated with latitudinal climatic adaptation, nonshattering infructescences or fruits among many crops, and reduced seed dormancy. He lists the following examples of predominantly human selection: Development of taller, less-branched plants leading to fewer, larger inflorescences, less spininess

(fewer thorns), reduced toxins, and attractive flower colors or patterns.

Natural selection for adaptedness probably caused cold resistance in high-altitude Peruvian maize, resistance to rust (caused by *Puccinia sorghi* Schw.) in high-altitude Mexican maize, resistance to leaf blight (caused by *Helminthosporium* spp.) in tropical Colombian maize, and long mesocotyls of certain Hopi maize cultivars (Mangelsdorf, 1974). Visual evaluation for earlier maturity, disease resistance, and ear and plant characters was effective for adaptedness. More recently, two new early-adapted hybrids were released for Pakistan (Saleem et al., 1997). Adaptation of a genotype to a specific thermal regime may be the consequence of long-term natural selection. Distinct germplasm groupings show specific adaptation to the lowland tropics, midelevation tropics and subtropics, the highlands, and temperate environments (Armstead et al., 1997). In the U.S. Corn Belt, the function of natural selection in corn is better adaptation to the conditions of life. The more important factors are probably those that differ markedly from Tehuacan, Mexico (18°N lat) near where corn originated in presumably ideal conditions for its life. Natural selection for adaptation to longer days, cooler minimum temperatures, shorter and drier seasons, and improved cultural practices occurred during and since the movement of corn to the USA.

Obvious examples of natural and human selection for adaptedness involve the increases in plant density and N application associated with the increase of U.S. corn grain yield. Mooers (1910, 1920) investigated adaptedness to plant densities of corn from 14 800 to 24 700 ha^{-1} (6000–10 000 acre^{-1}). Since that time, U.S. corn plant densities have increased steadily. Dr. J.W. Pendleton (personal communication, 2005) surveyed retired farmers in central Illinois and found the average corn plant density in the mid-1930s was 27 170 ha^{-1} (11 000 acre^{-1}). Jugenheimer and Troyer (1955) tested Illinois experimental corn hybrids at 28 224 and 38 730 ha^{-1} (11 760 and 15 680 acre^{-1}). An Illinois farm report shows mature corn plant densities of 63 726, 65 826, 65 084, 66 814, 68 419 ha^{-1} (25 800, 26 650, 26 350, 27 050, 27 700 acre^{-1}) for years 2000 to 2004, respectively (USDA-NASS, 2004b). Illinois plant densities and their trend for increase over time are typical for U.S. Corn Belt states (see Smith, 1998). Nitrogen application rates increased from 50 to 130 kg ha^{-1} (45 to 116 lb acre^{-1}) from 1965 to 1980 in the U.S. Corn Belt (Smith, 1998). Troyer and Rosenbrook (1983) recommend 15 and 25% above state-average plant densities for testing corn hybrids. Troyer (2000) recommends doubling local progressive farmers' average plant densities for selection during inbreeding. It takes time to develop inbreds and hybrids. Troyer (2004c) recommends increased N rates to increase variation for stalk quality.

Race Formation

Race formation in corn originated in southern Mexico about 7000 yr ago (Goodman, 1988). Prehistoric Native Americans selected for larger ears presumably to ease harvest and storage. The ancestors of Northern Flint races arrived in present day Arizona and New Mexico about 1000 BCE and moved slowly across the Great Plains probably from river valley to river valley to arrive in New England about 1000 CE (Goodman, 1988). By contrast, Spanish Conquistadors transported Southern Dent races from Mexico to present day Florida, South Carolina, and Virginia via Havana, Cuba, from 1539 to 1570 (Hudson, 1994). Northern Flint and Southern Dent races were separated geographically for 2500 yr and experienced different routes of travel with different conditions of life. They remain separated by flowering time.

The Northern Flints from New England have slender culms, irregular tillers (shoots at the base of the stem), well-developed flag leaves, and few visible brace roots and are of early maturity. Their leaves are long and slender and often light green in color. Their ears are cylindrical and 8 to 10 rowed, with strong thick shanks and proportionally larger cobs. Their kernels are wide, undented (hard starch), and not pointed. The tassels are wiry, with no condensation. The central spike bears its spikelets in whorls of two pairs: the pairs are 4-ranked and decussately arranged (at right angles to adjacent pair) on the spike (Table 1; Brown and Anderson, 1947).

The Southern Dents are taller because of more nodes with relatively shorter internodes than non-Southern Dent corns. Most Southern Dents have extremely short internodes just above the ear. Their leaves are relatively shorter and wider and often dark green in color. Ears are attached high on the culm (stalk) and are enveloped in tight, thick husks often extending well beyond the ends of the ears. Husks are usually modified leaf sheaths with the blade portion being only slightly developed. Typically, Southern Dents have no tillers although some derived cultivars occasionally produce a few tillers. Brace roots are well developed and may develop several nodes high on the culm when grown farther north. Their ears are cylindrical and 14 to 22 rowed, with slender shanks and proportionally smaller cobs. Their kernels are large, deep, rectangular to flat, usually white endosperm with softer starch that is dented. Tassels are highly branched and often highly condensed. Secondary branches of tassels are often upright and comparatively short and tertiary branches are in greater number than other corns (Table 1; Brown and Anderson, 1948).

Cultivar Formation

Crossbreeding Northern Flint and Southern Dent races to develop new cultivars showed benefits appreciated by a few experts as early as 1800 according to Wallace and Brown (1988), who cite authors Lorain (1813) and Browne (1837). By 1850, crossbreeding these two races was actively underway from Pennsylvania to Iowa and south to the Gulf States (Anderson and Brown, 1952; Wallace and Brown, 1988). Open-pollinated cultivars contain enormous amounts of variability for two reasons: Their backgrounds have adapted to many environments and cultural practices in 6500 yr of travel, and silk delay (tassel finishes shedding before silks emerge) forces cross pollination. Open-pollinated

Table 1. Some morphological traits of Northern Flint and Southern Dent races. (Brown and Anderson, 1947, 1948; AFT, personal experience).

Trait	Northern Flint	Southern Dent
Modern breeding	little	much
Yield level	low	high
Flowering date	earlier	later
Photoperiod preference	longer days	shorter days
Temperature preference	cooler	warmer
Physiological balance	usually source limited	usually sink limited
Stalk internode		
Number	fewer	more
Shape	longer, thinner	shorter, thicker
Pattern	progressively longer	progressively longer to ear attachment node where condensed, then progressively longer
Tassel		
Shape	smaller, wirier	larger, thicker
Branch number	fewer	more
Florets	sparser	more condensed
Leaf		
Number	fewer	more
Width	narrower	wider
Length	longer	shorter
Color	lighter green	darker green
Shank internode		
Shape	stout	slender
Length	longer, thinner	shorter, fatter
Number	fewer	more
Pattern	progressively shorter, not condensed	progressively shorter and condensed at ear attachment
Surface	ribbed	smooth
Ear attachment	larger	smaller
Husk		
Number	fewer	more
Width	narrower	wider
Cover	looser	tighter, bottleneck
Flag leaves	usually present	usually absent
Ear		
Shape	longer, thinner	shorter, thicker
Row number	fewer (8–10)	more (14–22)
Kernel		
Type	flintier	more dent-like, gourdseed
Size	small to large, wide	large, deep
Shape	round to flat, wide	rectangular to flat
Color	mixed	usually white
Texture	harder, corneous starch	softer starch
Test weight	higher	lower
Drying rate	slower	faster
Prop roots	usually absent	usually present
Tillers	usually present	usually absent
Cold germination test	very good	average to poor
Seedling growth	much faster	slower
Juvenile growth	faster	slower
Northern leaf blight	some tolerance	susceptible
Southern leaf blight	susceptible	some tolerance
Heat tolerance	susceptible	some tolerance
Cold tolerance	some tolerance	susceptible
Stay-green	less	more

cultivars were selected for more good ears, maturity, and other agronomic traits. Number of cultivars increased from 250 to 1000 during American westward expansion (Sturtevant, 1899; Montgomery, 1916). The Corn Belt moved from Tennessee, Kentucky, and Virginia in the 1830s; to Illinois, Ohio, and Missouri by 1858; and then to Iowa, Illinois, and Missouri by 1878. Iowa first produced more corn than Illinois in 1878. The 750 newer open-pollinated cultivars were earlier flowering and more tolerant to droughts, being adapted farther north and farther west (Montgomery, 1916).

Natural selection of persistent (longer lasting), popular open-pollinated cultivars Reid Yellow Dent, Minnesota 13, Lancaster Sure Crop, Northwestern Dent, and Leaming Corn occurred in Illinois, Minnesota, Pennsylvania, North Dakota, and Ohio, respectively. Reid Yellow Dent, Lancaster Sure Crop, and Leaming Corn were developed under higher yielding conditions while Minnesota 13 and Northwestern Dent were developed under lower yielding, stressful conditions with shorter, drier, cooler seasons. Improved persistent strains (Funk, Iodent, Osterland, and Troyer) of Reid Yellow Dent were developed in Illinois, Iowa, Iowa, and Indiana, respectively. Improved strains Richey Lancaster and Chester Leaming were developed in north-central and east-central Illinois, respectively. Each of these cultivars was also affected by different artificial (human) selection (Wallace and Brown, 1988; Troyer, 1999, 2004a).

Reid Yellow Dent was developed by Robert and James L. Reid in north-central Illinois from the cross of Gordon Hopkins cultivar, brought from southern Ohio, by Little Yellow cultivar from northern Illinois in 1847 (Wallace and Brown, 1988). Wallace and Brown (1988) refer to Gordon Hopkins cultivar as a gourd-seed or semi-gourd-seed dent and Little Yellow cultivar as an 8- to 10-row early flint cultivar grown by the Indians in the northeastern USA for many centuries. James L. Reid's handwritten account of the development is on file as an affidavit in the courthouse at Tazewell, IL. A verbatim copy is published in the 1907 Yearbook of Agriculture (Shamel, 1907).

According to Wallace and Brown (1988), James L. Reid selected for agronomic traits and for attractive ears. He selected medium-sized ears of medium maturity, with bright yellow kernel color and solid, deep, relatively smooth grain, with a small red cob, and with 18 to 22 kernel rows. James preferred ears being well filled over the tip and butt, leaving a small shank to ease hand husking. He saw vigorous plant growth and high shelling percentage as essential traits. James selected seed in the field at harvest time emphasizing mature, dry seed. Both Robert and James gave seed corn to their neighbors to keep Reid Yellow Dent pure.

Reid Yellow Dent is described as medium early relative maturity (115 RM) in the central U.S. Corn Belt. Stalks are rather heavy, tall, and leafy with above average ear height. Ears are 23 to 25 cm (9–10 in.) long, slightly tapered, well filled at the tips and butts, and have 16 to 22 closely spaced, dove-tailed, kernel rows on small, dark-red cobs with small shank attachment. Kernels are medium depth, thick, medium narrow width, slightly keystone in shape, square crowned, and smooth to rough indentation. Kernel color is bright, deep yellow with red tinges and a lighter yellow cap (Table 2; Shoesmith, 1910; Bowman and Crossley, 1911).

Lancaster Sure Crop was developed by the Hershey family near Lancaster, PA. They began with an early,

Table 2. Some morphological traits of Reid Yellow Dent and Lancaster Sure Crop cultivars (Shoesmith, 1910; Anderson, 1944; Wallace and Brown, 1988; Hershey, 1989).

Trait	Reid Yellow Dent	Lancaster Sure Crop
Seedling Vigor	good growth	very good growth
Stalk		
Plant height	taller	shorter
Ear height	above average	medium high
Leaf		
Type	leafy	fewer leaves
Color	dark green	lighter green
Ear		
Length	23–25 cm (9–10 in.)	25–30 cm (10–12 in.)
Shape	slightly tapered	long and slender
Tips and butts	well filled	filled
Kernel row no.	16–22 closely spaced	10–14
Shank	small diameter	large diameter
Cob		
Size	small	large
Color	dark red	white
Kernels		
Depth	medium for dent	deep for flint
Shape	keystone, thick, medium narrow width, square crown	large, rounded
Color	bright deep yellow, red tinges, lighter yellow cap	light to medium yellow
Indentation	medium to rough	smooth
Starch	soft	flinty

slender, smooth, usually single-eared corn obtained from the U.S. Patent Office in 1860. Isaac, helped by his brother Benjamin, selected among harvested ears in the seed house because corn in the area was shocked to help dry the ears and to use the stalks for fodder. He preferred medium-length, well-matured, sound ears with clean shanks and with neither moldy nor silk-cut kernels. Isaac repeatedly selected smooth, flinty ears after out crossing to later dent cultivars. At a later date, Isaac's son Noah selected for stronger roots and larger ears in fields of standing corn. Over time Lancaster Sure Crop was crossed to later dent cultivars then crossed back to Lancaster Sure Crop 8 to 12 times, by mixing seed at planting, followed by selection for flintier, smoother, longer ears at harvest. The Hershey family started selling seed in 1910, when they quit crossing and blending their seed and began selecting for more uniformity (Table 2; Anderson, 1944; Hershey, 1989).

Lancaster Sure Crop was so named because of earlier-than-average maturity and drought tolerance. It is medium early (112 RM) for the central U.S. Corn Belt. Ears are 25 to 30 cm (10–12 in.) long, slender, smooth, and have 10 to 14 kernel rows, white cobs, and larger diameter shanks. Kernels are light to medium yellow, large, deep, rounded, and flinty. Plants are tall with medium-high ear height and only average root and stalk strength (Table 2; Anderson 1944, Wallace and Brown, 1988).

Anderson (1944) documented the old breeders' tale that much of the corn being grown in the USA traces back to Reid Yellow Dent and Lancaster Sure Crop cultivars (Table 2). Krug and Lancaster Sure Crop are both smoother eared utility type, *not* show type, cultivars. Anderson expected Krug cultivar to be better adapted than Lancaster in the present U.S. Corn Belt because of natural selection (place of development). Krug cultivar

was recommended in five central states and Lancaster Sure Crop cultivar was recommended in five eastern states in 1936 (Jenkins, 1936). Anderson may not have known of Richey Lancaster, which was grown in north-central Illinois for some decades and then taken to Iowa State and Ohio State Experiment Stations by F.D. Richey in 1922 (Crabb, 1948; Jenkins, 1978; Troyer, 1999). Modern Iodent inbreds developed by Raymond Baker obtained their longer ears (higher yield) from Richey Lancaster Iowa inbred LAN (Troyer, 2004a).

Funk and Troyer Reid cultivars were selected for more deeply dented kernels on show-type ears. Troyer Reid was developed on subirrigated, river-bottom fields where natural selection would favor better, deeper rooting. Funk Strain 176A, a smooth-eared utility corn, was developed from Funk Reid. Dr. Jim Holbert's selection emphasized cold-test germination and disease resistance. Lancaster Sure Crop and Richey Lancaster are more flint-like in ear and plant traits than Reid Yellow Dent (Table 2; Troyer, 1999).

Better adaptedness, particularly of Reid Yellow Dent, Minnesota 13, Lancaster Sure Crop, Northwestern Dent, and Leaming Corn cultivars, accounts for much of the increased average yields and total production over time in the background of improved hybrids in the USA. Selection for more widely adapted hybrids ultimately favored germplasm from the more popular, widely grown, open-pollinated cultivars containing more genes for adaptedness to the U.S. Corn Belt (Allard, 1988; Vladutu et al., 1999; Tuberosa and Phillips, 2002; Troyer, 1999, 2004a, 2004c). Natural and artificial (human) selection for adaptedness to different conditions of life causes the genotypic differences between parents that cause heterosis (Darwin, 1859; Moll et al., 1962). It should be fruitful to study the gene action causing adaptive traits (Allard, 1988; Vladutu et al., 1999; Tuberosa and Phillips, 2002).

Heterosis

Heterosis is poorly understood. Several prominent speakers including Drs. Coors, Duvick, Edwards, Hallauer, Lamkey, Lee, Rashid, and Stuber point out that little of substance has been learned in the last 50 yr that explains heterosis. Their comments, which appear only in the Conference on Heterosis Book of Abstracts (CIMMYT, 1997), were the incentive for this paper. Despite the use of potentially predictive databases and statistical procedures for estimating single cross performance, corn breeders must make thousands of crosses to find a few superior commercial hybrids. Smith (1997) states that Pioneer Hi-Bred International generates 6000 single crosses to test at 15 to 20 locations annually in part to predict newer, additional single crosses. It is a cut-and-try process; predicted hybrids must then be tested extensively before being sold. Phillips (1999) suggests the need to go beyond the thought of heterozygosity of a collection of individual genes.

Calculating heterosis percentage and heterosis per se is troublesome because parent inbred yield is a conundrum: Increasing parent inbred yield for improved single-cross hybrid seed production decreases heterosis

values when hybrid yield is held constant. Heterosis per se equals hybrid yield minus parent inbreds' average yield. Percentage of heterosis equals heterosis per se divided by parent inbreds' average yield. Higher parent inbred yields directly reduces the dividend (heterosis per se) and increases the divisor (parent inbreds average yield) thus decreasing the quotient (percentage of heterosis). Increased inbred parent yield reduces heterosis per se in the first formula and reduces percentage of heterosis via both sides of the ratio in the second formula. The breeder's goal is higher yielding hybrids that are produced from higher yielding, commercially productive inbreds.

Heterosis increases corn yields. Figure 1 shows the association of cultivars, types of hybrids, biotechnology, and cultural practices on U.S. average yield increases of corn over time. United States corn yields have increased from 1518 kg ha^{-1} in the 1930s when hybrid corn was available commercially to 10 059 kg ha^{-1} at present (24.2 to 160.4 bushels acre^{-1}). United States annual corn production has increased from 53 million Mg to 299.7 million Mg [2 billion (2×10^{-9}) to 11.8 billion bushels] on 22% *less* surface area planted since hybrid corn became available (Fig. 1; USDA-NASS, 2005). Planting of biotech cultivars for 2000 to 2004 are 25, 26, 34, 40, and 45% of all U.S. corn area planted (USDA-NASS, 2004a). The yield regression associated with biotech for the past 10 yr is 207.2 kg ha^{-1} (3.30 bushels acre^{-1}) yield increase per year.

Heterosis change over time is of interest. Duvick (1999) presents experiments designed to compare yields of important inbreds with their single-cross hybrids over a time series. All trials were grown in the U.S. Corn Belt, where the inbreds were highly successful in hybrids for some period of time. His results simulate progress during five decades in one experiment and six decades in another. My Fig. 2 and Table 3 combine experiments 2 and 3 from Table 3–2 (Duvick, 1999). My data for the 1980s are from Experiment 3 only (Duvick, 1999). My Fig. 2 graphs the combined results in percentage of 1930s performance to show breeding gain since hybrid corn: Hybrid yield increased 3894 kg ha^{-1} (62 bushels acre^{-1} or 74%) over 60 yr. Heterosis per se increased 1414 kg ha^{-1} (22 bushels acre^{-1} or 44%). Percentage of heterosis was relatively constant, averaging 57% and declining 2% per decade over time. The relative constancy of percentage of heterosis for yield in adapted, successful corn hybrids occurs because the hybrid and its inbred parents are affected by the season in like manner due to their mutual adaptedness. Of particular note, inbred yields (no heterosis) increased 2479 kg ha^{-1} (39 bushels acre^{-1} or 122%) over 60 yr (Fig. 2; Table 3). Many favorable alleles for grain yield have been accumulated in individual parent inbreds.

Old inbreds have notoriously poor agronomic traits: Poor germination causes poor stands; silk delay causes poor pollination; weak roots, broken stalks, and moldy ears, etc., further reduce yield (Baker, 1984). Corn breeders saw these faults as opportunities. Better inbreds made better hybrids. Additive, dominance, and epistatic gene action for agronomic traits were exploited.

Duvick's (1999) regressions for *actual rates of gain* per year for yield favor the larger, higher yielding hybrids; however, the smaller, lower yielding inbreds gain faster in *percentage of gain* for yield. If the trends in percentage of gain continue, inbreds that yield more than hybrids may occur within the present century. The slightly declining trend for percentage of heterosis is caused by inbreds increasing more rapidly than hybrids in percentage of yield over time (Fig. 2; Table 3). Much of the risk of single-cross, seed-corn production has been reduced by the development of higher yielding inbreds with better adaptedness to the environment and cultural practices (Fig. 2; Table 3; Duvick, 1999).

Controlled heterosis in hybrids accompanied on-farm corn yield increases since 1930. Figures 1 and 2 relate to the same increase in U.S. corn yields over time. The figures differ as follows: Fig. 1 is what actually happened. Each point on the graph is the result of then-current hybrids with then-current cultural practices. Figure 1 documents the actual U.S. average corn yield year by year. About 50% of the gain in yield over time is due to improved cultural practices (Russell, 1991). Figure 2 simulates an estimate of gain through six decades (1930 to 1980) based on hybrids made with successful inbreds. The hybrids and their parent inbreds were grown simultaneously in the same tests to provide comparable yields. Because the trials were grown recently, modern cultural practices were necessarily used. Therefore, all gains in Fig. 2 and Table 3 are breeding gains since the introduction of commercial hybrid corn in the 1930s up to the specified decade.

Evolution of Heterosis

Natural selection improves the adaptedness of plants to the conditions of life (evolution). In a similar manner, corn breeders use human (artificial) selection for the highest harvestable yield over a large number of locations. Both types of selection affect survival and differential reproduction to increase number of individuals (seeds) available for the next generation. Better adapted plants develop more viable seeds; they are higher yielding. Darwin (1875) described the advantage of cross-pollinated over self-fertilized plants under stress as follows: "To my surprise, the crossed plants when fully grown were plainly taller and more vigorous than the self-fertilized ones. The crossed plants had a decided advantage over the self-fertilized plants under this extremity of bad conditions." Heterosis is more pronounced under stress. Natural selection for adaptedness favored cross-pollinated plants in corn races and open-pollinated cultivars. Silk delay was the mode of action to provide more vigorous, cross-pollinated progeny. Because crossing was advantageous, heterozygosity became and still is an important cause of heterosis (vigor). Hybridization of hybrid corn causes a greater number of heterozygous loci just as cross pollination in races and varieties did.

Duvick (1997) suggests that heterosis may only be a catalyst (provokes or speeds change or action) for increasing yields of hybrid crops. Percentage of heterosis is
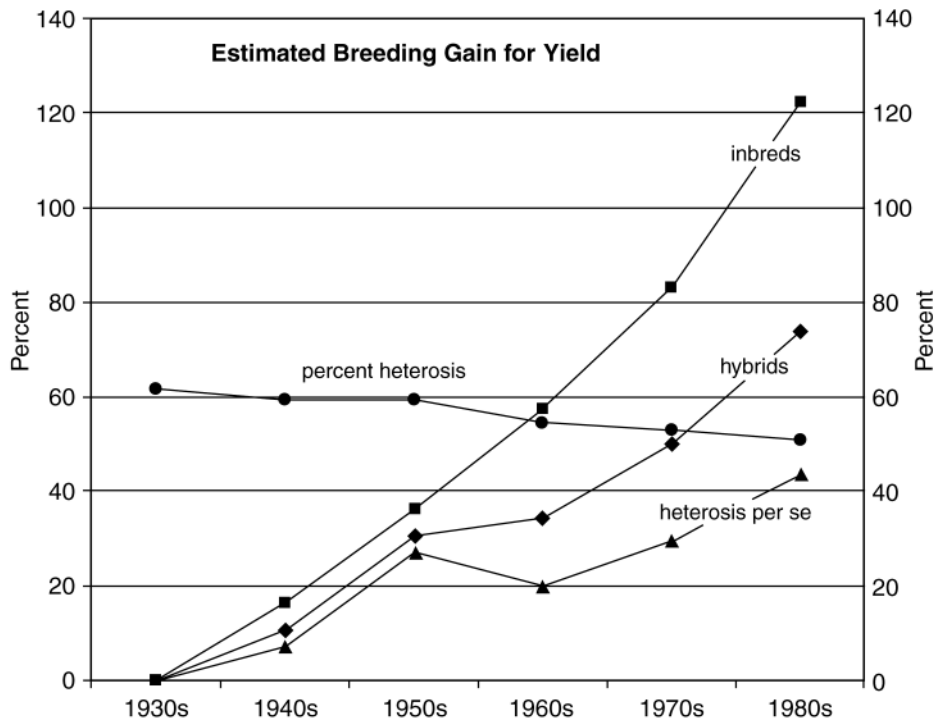
Fig. 2. Yields of single-cross hybrids, their inbred parents, and heterosis per se over six decades in percentage of 1930s values. Percentage of heterosis is in actual values for each decade. From combined Experiments 2 and 3 in Table 3–2 (Duvick, 1999).

calculated as a ratio of heterosis per se and average yield of parent inbreds. Percentage of heterosis in U.S. hybrid corn is decreasing slightly (~2% per decade) because inbred yields in percentage are increasing faster than hybrid yields in percentage (Fig. 2; Table 3). Increased yield of parent inbreds decreases cost and risk of single-cross hybrid seed corn production. In addition, heterosis will probably not exceed some maximum level because of plant physiological (size of plant, etc.) and/or environmental (length of season, number of heat units, etc.) limits.

Genetic Diversity

Tens of thousands of corn cultivars are presently maintained by germplasm banks (Labate et al., 2003). A great many have been self-pollinated in attempts to develop useful inbreds because genetic diversity has been a common goal. Some breeders routinely screen foreign, unusual cultivars. Genetic diversity increases yield in a linear fashion up to an optimal limit (Moll et al., 1962, 1965). A successful parent must have some degree of adaptedness to the area where the hybrid is grown. Genetic diversity values between two hybrids can be estimated by scaling their hybrid F1 (the cross of the two hybrids) yield between the average of their two F2 yields and the average of their two per se yields (Troyer et al., 1988). This requires about as much time and effort as evaluating five inbreds on one tester. Hallauer and Williams (2000) compared genetic diversity values with Nei's genetic distance and found caution necessary to interpret them relative to each other. They recommend starting with Nei's genetic distance followed with genetic diversity values if additional information is required. Genetic diversity may increase yield ascribed to heterosis in at least two ways: More genetic diversity may increase the hybrid's area of adaptedness over a larger geographic area, and it may increase heterozygosis because diverse geographic areas favor different traits thus different genetic loci are affected. Farmers' past concern about genetic diversity has lessened over time as evidenced by the popularity of

Table 3. Hybrids, parent inbreds, and heterosis per se yields; and percentage of heterosis for six decades. Breeding gain for yield 1930s to 1980s in kg ha^{-1} and in percentage. From combined Experiments 2 and 3 in Table 3–2 (Duvick, 1999).

	Decade						Breeding gain 1930 to 1980	
Source	1930	1940	1950	1960	1970	1980		
	kg ha^{-1}						kg ha^{-1}	%
Hybrids	5270	5835	6882	7087	7914	9164	3894	74
Parent inbreds	2027	2359	2761	3192	3714	4506	2479	122
Heterosis per se	3244	3477	4122	3894	4201	4658	1414	44
Percentage of heterosis	61.5	59.5	59.5	54.5	53.0	51.0	–	−10

more widely adapted hybrids that interact less with seasonal weather (Troyer, 1996).

Heterotic Gene Action

Shull (1908) presented the first theory of heterosis based on the premise that heterozygosity per se was the cause. East and Hayes (1912) state: "The greater the degree of heterozygous condition the greater is the vigor of the resulting plant, and the decrease in vigor due to inbreeding lessens with decrease in heterozygosity and vanishes with isolation of a completely homozygous strain." Shull (1948) states: "In 1914, I proposed the word heterosis to replace the more cumbersome word 'heterozygosis' which had been found useful by a few geneticists of that time, myself among them." Knight (1948) defines heterozygosis as the state of being heterozygous; that is, formed from the union of gametes of dissimilar genetic constitution. *Dictionary of Genetics* (Knight, 1948) and *A Dictionary of Genetics* (King, 1972) see heterozygosis as a synonym for heterozygosity, but Shull relates heterozygosis specifically to heterozygosity causing heterosis. East and Jones (1919) state: "The heterozygosis hypothesis satisfies all the essential facts of heterosis and inbreeding depression; it is only necessary to postulate developmental stimulation from different germplasm." Hageman et al. (1967) state: "Heterozygosis provides a more favorable genetic constitution for enzymatic efficiency."

Fred Hull, successful breeder of two inbreds in popular Dixie 18 (Troyer, 2004b), became concerned that second-cycle inbreds performed poorly in hybrids. Developing superior newer inbreds was more difficult than he expected. He suggested the term overdominance for superior heterozygous loci and suggested recurrent selection with early testing (unfinished inbreds) for specific combining ability as a procedure to breed for such gene action (Hull, 1945, 1952). Early testing is extra testing—the finished inbred must be tested again at or near homozygosity. At about the same time, Richey (1945), successful breeder of one inbred each in Hoosier Hybrid and in Copper Cross Hybrid (Troyer, 2004b), suggested recurrent selection with late testing (finished, homozygous inbreds) as cumulative selection. Late testing requires less yield testing per finished inbred. He emphasized selection for general combining ability. Richey's scheme was an observation of what appeared to be happening over time. More vigorous inbreds over time that reduce percentage of heterosis (Fig. 2, Table 3) lessen the likelihood of much overdominance in hybrids (Hull, 1945; Crow, 1948, 1952). Crow (1997, 1999) states: "It is unlikely that overdominance gene action is making any large contribution to heterosis; dominance is more important."

Stringfield (1950) compared the average yield of the two possible first backcrosses with yield of the F2. This provides identical average gene frequencies for the two (BC1 and F2) types of populations. His materials were a four-inbred diallel set of six possible single-cross hybrids. The average of the backcrosses yielded 4258 kg ha^{-1} (67.9 bushels acre^{-1}), and the F2s yielded a significantly less 3900 kg ha^{-1} (62.2 bushels acre^{-1}). The backcross plants each have a complete chromosome complement from the recurrent parent inbred—the F2 plants do not (Sharp, 1934). Stringfield (1950) states: "Inbreds surviving the selection procedure may tend to have favorable combinations of genes contributing more vigor than a random assortment individually just as good."

Within-inbred, favorable epistasis causes single-cross hybrids to be higher yielding than more complicated hybrids. Weatherspoon (1970) measured grain yield of 108 hybrids including a balanced set (equal gene frequencies) of 36 single, three-way, and double-cross hybrids involving nine unrelated inbreds. The 108 hybrids averaged 6247 kg ha^{-1} (99.3 bushels acre^{-1}). The 36 single-cross hybrids yielded 6510 kg ha^{-1} (103.5 bushels acre^{-1}), the 36 three-way hybrids yielded 6200 kg ha^{-1} (98.6 bushels acre^{-1}), and the 36 double-cross hybrids yielded 6030 kg ha^{-1} (95.9 bushels acre^{-1}). Single crosses (two inbred parents) are grown annually on nearly all of ~30.4 million hectares (75 million acres) in the USA. Hybrids with three or four parent inbreds are much easier for seed-corn production, but single-cross hybrids yield more in farmers' fields. Single crosses require higher yielding parent inbreds for practical seed production. One might expect within-inbred favorable epistasis to evolve had it not already been present because it increases the yield of both parent inbreds and their hybrid. Within-inbred, favorable epistasis, where both inbred parents' complete chromosome complements are in each hybrid plant, explains single-cross hybrid's superior yield (Sharp, 1934). Three-way hybrids have one complete parent chromosome complement in each hybrid plant. Double-cross hybrids have none because of recombination (crossing over and independent assortment) during meiosis (Sharp, 1934; Stringfield, 1950; Weatherspoon, 1970; Troyer, 2000, 2004a, 2004d).

Better ways of measuring and predicting within-inbred, favorable epistasis are needed. Use of heterotic groups and general combining ability in choosing closely related inbreds to cross for inbreeding are helpful to maintain and to increase within-inbred, favorable epistasis (Troyer, 1990, 2000; Allard, 1997; Hinze and Lamkey, 2003). By contrast, sib mating disrupts existing within-inbred, favorable epistasis. Favorable epistatic gene action may become fixed and maintained in inbreds (Lamkey et al., 1995). Utilizing within-inbred, favorable epistasis offers a more controlled and predictable breeding method for inbred or hybrid improvement (Troyer, 1994, 2000; Lamkey et al., 1995).

Heterozygosis continues to be the simplest explanation of heterosis; that is, the increased vigor of the F1 hybrid. Natural selection for adaptation during the evolution of corn has been the main cause. Corn is *not* unique in this regard—other organisms display hybrid vigor (see Mule Hybrids below). By contrast, human selection explains the increased vigor (yield) of newer, homozygous inbreds. Hybrid corn breeding selection criteria have simultaneously increased yields of inbreds and hybrids. Many of the useful human selection traits in inbred development are expressed by additive, dominant, or epistatic gene action in hybrids. The breeder's

ultimate goal is to improve the hybrid. In addition, more vigorous, higher yielding parent inbreds more reliably and more profitably produce hybrid single-cross seed — it's good for business. The newer homozygous inbreds are much more vigorous (higher yielding). Many higher yielding inbreds resulted from inbreeding popular commercial hybrids that were well adapted thus giving forth better adapted newer inbreds (Troyer, 2004a).

Heterotic gene action in corn has received much attention (see Hallauer and Miranda, 1981; Hallauer et al., 1988; Allard, 1999; Crow, 2000). A prolonged debate has taken place during the past century between advocates of the overdominance or physiological stimulation theory versus the dominant favorable growth factors theory. Although corn breeders have taken an active part, the debate has been largely academic. Lamkey and Edwards (2004) state: "The debate over type of gene action controlling heterosis was the stimulus for much of the quantitative genetics research conducted since the 1940s." The old original heterozygosis theory (Shull, 1908) coupled with corn history and evolution (adaptedness) is more understandable and more useful to corn breeders. The heterozygosis theory supports the overdominance theory; they differ only in number of loci. The increased inbred yields in Fig. 2 and Table 3 support the dominant favorable growth factors theory. Dominance, additive and epistatic effects are more noticeable and more traceable in a hybrid crop. Multiple types of gene action increase yields of hybrid corn.

Corn Hybrids

Dr. W.J. Beal measured hybrid vigor in crosses of open-pollinated cultivars at Michigan State in 1878. He called the crosses mule corns. George Morrow confirmed Beal's results and suggested today's production method at the University of Illinois in 1892 and 1893 (Morrow and Gardner, 1893, 1894). Professor Perry Holden, the great corn evangelist, and Wilbur J. Fraser, an undergraduate, who later became Dairy Department Head at Illinois, started the first inbred development that resulted in commercial hybrid corn in Chester Leaming cultivar at Illinois in 1895. Professor Holden was the first to cross corn inbreds in 1898, and he first observed single cross hybrids in 1899 (Wallace, 1955; Troyer, 2003). Edward M. East first grew the previously bulked Illinois inbreeding materials ear-to-row. He left Illinois to further study inbreeding of corn at the Connecticut station in 1905. He obtained Chester Leaming inbreds from Illinois to grow in 1906 (Crabb, 1948). Dr. G.H. Shull delivered an address on "The composition of a field of maize" to the American Breeders Association in 1908 (Shull, 1908). Herbert K. Hayes at Connecticut obtained Burr White chemical composition selections from Illinois for his Ph.D. thesis study (Troyer, 2003). East made hybrids that yielded more than 12 543 kg ha^{-1} (200 bushels acre^{-1}) in 1908 and 1909 (Troyer, 2003). Dr. C.G. Hopkins proved the efficacy of inorganic fertilizer (Hopkins, 1913).

Dr. D.F. Jones produced the Burr-Leaming double-cross hybrid in Connecticut in 1917; it was first produced commercially in 1921 (Jones, 1927). Drs. A.L. Lang and J.W. Pendleton led innovation of improved cultural practices (Lang et al., 1956). Single-cross hybrids became more popular from the mid-1960s through 1980. Popular, widely adapted hybrids grew in favor from the 1970s through 1990. Widely adapted corn hybrids were achieved by using wide-area testing, high plant density stress for selecting inbreds and screening hybrids, and modern information management that equalized location effect and provided pertinent comparisons (Bradley et al., 1988; Troyer, 1996, 2003, 2004b).

Combining Ability

Hayes and Immer (1942) defined combining ability as the relative ability of a biotype to transmit desirable performance to its crosses. Inbreds must yield enough to make seed corn production profitable (Hayes and Garber, 1921). Richey (1924) and Richey and Mayer (1925) found that certain inbreds gave higher yielding crosses. Jenkins (1929) obtained a multiple correlation of 0.42 using four characters (plant height, number of nodes per plant, number of nodes below the ear, and inbred yield) to predict hybrid grain yield. Davis (1929) first suggested the use of top crosses (open-pollinated cultivar tester) to test combining ability. Hayes and Johnson (1939) obtained a correlation of 0.67 using 12 characters (date silked, plant height, ear height, leaf area, pulling resistance, root volume, stalk diameter, number of brace roots, tassel size, pollen yield, plant yield, and ear length) to predict hybrid grain yield. On average, the more vigorous inbreds were better combiners (yielded more in hybrids) than the less vigorous inbreds. Hayes and Johnson (1939) state: "A great deal of information indicates that some inbreds combine well in top-crosses or with unrelated inbreds whereas other inbreds have lower combining ability. When comparing inbred to hybrid correlations, the correlations are higher [more useful] when comparing inbred yield to the average yield of their hybrids."

Sprague and Tatum (1942) defined general and specific combining ability from diallel (all-possible) crosses of 10 inbreds. General combining ability is measured as though it were due to additive gene action. Specific combining ability includes all effects which cannot be accounted for on the additive scheme. These may be the result of dominance, epistasis, genotype by environment interactions, etc. Reporting specific combining ability and general combining ability in percentage of yield test location mean allows valid comparisons (postulating best hybrids in yield tests) across locations and years for hundreds and even thousands of location–tester environments. Use of the t test to compare performance values with the mean (100%) correctly identifies better and worse than average performance for each trait of each inbred. Hallauer (personal communication, 2004) states: "Different genetic effects make [specific combining ability] unique for each cross making extensive testing necessary to find the best single-cross hybrid." The two best adapted (highest general combining ability for yield or yield to moisture) unrelated inbreds for an

area often parent the best hybrid for that area (AFT, personal experience).

Heterotic Groups

Heterotic groups are formed by isolation and selection (natural or human) for adaptedness over time (Darwin, 1859). Their isolation from each other may be different geography, different flowering time, or hand pollination. Selection may be natural and/or artificial (human) to increase the frequency of alleles associated with adaptedness for the area of use. Easier harvest and storage presumably drove human selection for larger ears by Native Americans. Land ownership probably drove human selection for higher yield per unit area of land in the American Colonies. Seed corn pricing by the ear, corn shows, moderate plant densities, and hand harvest drove selection for larger, attractive ears during American westward expansion. Desire for less hybrid interaction with seasons drove human selection for widely adapted, popular hybrids (Troyer, 1996).

Probably the most productive thesis problem of all time, "Relation of stalk and ear characters to yield in Reid Yellow Dent," was conducted under Professor H.D. Hughes at Iowa State by Benjamin Duddleston (1918). After a short period in the U.S. Navy near the end of World War I, Duddleston joined the USDA at Purdue University and developed the all-time most popular inbreds out of improved derivatives of Reid Yellow Dent. Purdue inbred WF9 from Wilson Farm Reid (Wilson Farm was the Purdue Agronomy Research Farm near Lafayette, IN) was grown in hybrids on 30% of U.S. corn acreage for 30 yr. Using $29.5 billion for the 2004 crop value times 30 yr times 30% divided by four (1/4 of each) equals $66 billion. Later, it was a parent of the first popular single-cross hybrid WF9 × C103. Purdue inbreds 461–3, B164, B2, TR, and probably FE from Troyer Reid were also popular. Five of Ben Duddleston's inbreds, seven of Dr. Merle Jenkins, and eight others with one developer each were in the background of Stiff Stalk Synthetic developed by George Sprague in the early 1930s. Fifteen of the 20 (75%) inbred components had Reid Yellow Dent backgrounds (Hallauer et al., 1983; Hallauer, 2002; Troyer, 1999, 2004a).

Particularly useful Iowa inbreds from Stiff Stalk Synthetic include B14, B37, and B73, which were 9, 26, and 16% of total U.S. seed requirements in years 1971, 1971, and 1980, respectively. Inbreds B14 and B37 were developed by Dr. George Sprague. Inbred B73 was developed by Drs. Wilbert Russell and Lowell Penny. Hallauer et al. (1983) state these three elite inbreds became the parents of more than 100 useful inbreds. More recently, inbreds B73 and B14 were in the background of 116 and 52 useful inbreds, respectively in the MBS 2000 Genetics Handbook (Hallauer, 2002).

Heterotic Patterns

Heterotic patterns are the relative performance of crosses of heterotic groups. Anderson and Brown (1952) state the Northern Flint and Southern Dent corn races are so different that, were they wild grasses, they would certainly be assigned to different species and perhaps to different genera. They state the heterosis of Corn Belt maize seems to be due to the mingling of Northern Flints and Southern Dents, and the greatest heterosis could be expected to result from crosses between inbreds resembling the Southern Dents with inbreds resembling the Northern Flints. Successful parent inbreds should resemble adapted U.S. Corn Belt corn, but morphological characters of Northern Flint and Southern Dent races may help predict superior hybrids. Anderson and Brown (1952) used morphological traits (row number, kernel width, and husk leaf blade size) to obtain a correlation of 0.40 in predicting hybrid grain yield. They might suggest that Smith (1997) could predict new superior hybrids with fewer than the present 6000 single-crosses grown by not testing the ones with similar morphological traits. The complexity of predicting heterosis in corn arises from the more than 40 morphological differences between Northern Flints and Southern Dents each signaling genetic differences (Table 1; Troyer, 1999, 2004a).

Corn heterotic patterns are determined empirically between heterotic groups (Hallauer et al., 1988). Dr. G.F. Sprague (personal communication, 1993) first noticed the Reid Yellow Dent by Lancaster Sure Crop heterotic pattern while writing the late Dr. A.A. Bryan's 1939 and 1940 USDA corn breeding annual reports at Iowa State. Anderson and Brown (1952) state: "Lancaster Sure Crop has a stronger infusion [background] of Northern Flints than most Corn Belt cultivars, and superior heterosis [better hybrids] is more likely to be found among the best flints [flint-like plant morphology]." Reid Yellow Dent and Lancaster Sure Crop cultivars differ morphologically as follows: Lancaster Sure Crop cultivar has a shorter plant with fewer leaves that are lighter green in color. Lancaster Sure Crop ears are 2.5 to 5.0 cm (1–2 in.) longer and more slender with six to eight fewer kernel rows and larger shank attachment. Lancaster Sure Crop kernels are smoother, larger and rounder shaped with harder starch and lighter yellow color. Lancaster Sure Crop cobs are white and Reid Yellow Dent cobs are dark red. Reid Yellow Dent is more Southern Dent like and Lancaster Sure Crop is more Northern Flint like for all the aforementioned traits (Table 2).

Jenkins (1978) heralded the importance of Lancaster Sure Crop (actually Richey Lancaster) cultivar by pointing out that Iowa inbred L289 was in hybrid Iowa 939 and Iowa inbred L317 was in hybrid U.S. 13. These were the first two most popular double-cross corn hybrids (Jenkins, 1978: Troyer, 1996). A sister inbred from Richey Lancaster, Iowa inbred L304A, was in commercial hybrid Troyer L11 (C.E. Troyer, personal communication, 1960). Hybrid Troyer L11 attained the all-time highest grain yield in the Illinois Commercial Corn Tests (Leng and Finley, 1956). The tests began in 1934 (Dungan, 1935) and continued 28 yr through 1961 (Leng and Ross, 1962). Since then, Lancaster inbreds OH43 (from Richey Lancaster and Northwestern Dent background) and C103 (Lancaster Sure Crop background) and their derivatives have been parents of many

outstanding hybrids (Troyer, 1996, 2004a), and then inbred MO17 followed by LH51 (both with 10-rowed, flint-like ears from Lancaster Sure Crop and Krug background) followed by inbred LH123 (from Pioneer hybrid 3535). Inbreds MO17 and OH43 were in the background of 46 and 42 useful inbreds, respectively in the MBS 2000 Genetics Handbook (Hallauer, 2002). Use of the Reid Yellow Dent by Lancaster Sure Crop heterotic pattern has been and still is popular (Table 2).

Hybrid B73 × MO17 was one of the all-time most popular central U.S. Corn Belt hybrids. It was developed by Drs. W.A. Russell, L.H. Penny, and A.R. Hallauer at Iowa State. It probably sold more than 15 million bags in spite of being difficult to produce, not sold by Pioneer Hi-Bred International (AFT, personal experience), and too late in maturity for the northern U.S. Corn Belt (Troyer, 2004b). The parent inbreds differ morphologically (Table 4) as follows: Inbred B73 germinates and emerges 19% better and grows faster in the seedling stage. B73 has 9% higher ear height, 10% longer leaves, and one more leaf above the ear. B73 has 6° and 15° more erect leaf and tassel branch angle, respectively. B73 is darker green. B73 ears are upright; have six more kernel rows and six fewer kernels per row with 21% and 40% more ear and cob diameter, respectively; and have 15% more weight per ear. B73 kernels are 9% longer. Inbred MO17 has 22% longer tassel, 26% longer spike, and 25% longer peduncle. MO17 ears are pendulant and have 46% longer shanks. MO17 ears are 27% longer. MO17 kernels are 9% wider, 14% thicker with 6% more weight per 1000 kernels. MO17 has 6 points higher shelling percentage. They have similar anthesis (pollen shed) dates; MO17 has a long silk channel (long husks) often causing silk delay in dry weather. This causes the need for two planting dates of the male when MO17 is used as the female for seed production.

Inbred MO17 is the presumed Northern Flint type. It should germinate better and show more spring vigor, but it does not because of a thin, delicate pericarp (seed coat) and large round kernels that poorly protect the germ face (AFT, personal experience). MO17 is lighter green, lower ear attachment, longer shanks with kernel and ear traits of Northern Flint type. By contrast, B73 is more Southern Dent like for these aforementioned traits (Table 4). Hallauer et al. (1988) point out the contrast of ear length, number of kernel rows, and total number of kernels per ear between the inbred parents of this hybrid. Perhaps a sightless person with a modicum of reasoning ability might feel an inbred MO17 or inbred C103 ear and suggest it should be crossed to an inbred with ears of higher kernel row number, deeper kernels, and softer endosperm starch to obtain a higher yielding hybrid. It's rather intuitive to one who has thought about it.

Mule Hybrids

Mules were the prototype for hybrid corn. They are the progeny of a female horse and a male donkey. After an excellent description of hybrid corn, Sinnott and Dunn (1939) state the mule is perhaps the most famil-

Table 4. Some morphological traits of Inbreds B73 and MO17 (DEKALB Genetics Inc.)

Trait	B73	M017	Difference
		AVG	% of mean
Seedling			
Percent emergence	91	75	19
Height, cm	45	41	9
Vigor rating†	3	5	50
Stalk			
Plant height, cm	212	208	2
Ear height, cm	92	84	9
Diameter (width), cm	3	2	40
Anthocyanin	weak	weak	
Nodes with prop roots	2	1	67
Prop root Color	dark		
Internode direction	straight	straight	
Internode length, cm	12	13	8
Pre-anthesis brittle snap, %	0	0	
Pre-anthesis root lodge, %	0	0	
Leaf			
Angle from vertical	30	36	18
Number			
Number above ear	6	5	18
Post flowering color	dark green	medium green	
Length, cm	74	67	10
Width, cm	9	9	
Sheath pubescence	4	1	120
Marginal waves	4	4	
Longitudinal creases	3	3	
Tassel			
Total length, cm	36	45	22
Spike length, cm	20	26	26
Peduncle length, cm	7	9	25
Attitude	compact	compact	
Branch angle from vertical	23	38	49
Branch number	7	6	15
Anther color	pink tan	yellow green	
Ear			
Silk color	yellow green	pink tan	
Number per stalk	1.0	1.0	
Position (attitude)	upright	pendulant	
Length, cm	14.0	18.3	27
Shape	short, thick	long, slender	
Diameter, cm	4.3	3.5	21
Weight, g	109.8	94.9	15
Shank length, cm	7.6	12.2	46
Husk			
Bract	short	short	
Cover, cm	7.2	2.5	97
Opening	3.7	2.7	31
Color fresh	green	green	
Color dry	buff	buff	
Cob			
Diameter, cm	2.7	1.8	40
Color	red	red	
Shelling, %	80.2	86.2	7
Kernel			
Row number	16.8	11.2	40
Number per row	25.7	32.4	23
Row direction	curved	straight	
Type	dent	dent	
Cap color	yellow	yellow	
Side color	orange	orange	
Length (depth), mm	11.3	10.3	9
Width, mm	7.2	8.5	9
Thickness, mm	4.1	4.7	14
Weight of 1000 kernals, g	266.8	283.8	6
Endosperm type	normal	normal	
Endosperm color	yellow	yellow	
Uniformity ranking†	3	3	
GDU to 50% pollen shed	1500	1514	1
GDU to 50% silking	1563	1646	5

† 1–9 scale with 1 being the best.

iar example of a hybrid and its vigor. Even later, Rice (1942) states mules are still the best known hybrid organism in the USA. More than five million mules existed in the USA when George Carter produced the first commercial double-cross hybrid seed corn in Con-

necticut in 1921 (Williams and Speelman, 1938). Three broad categories of mules are bred including: northern large mules for draft mules, southern medium mules for cotton (Mississippi and Alabama) or sugar (Louisiana and Georgia) mules, and small mules for shaft mining (Telleen, 1977). Mule breeders have used heterotic patterns for millennia to accurately predict the mature size and weight of hybrid animals. Corn breeders use heterotic patterns (less accurately) to predict higher yielding corn hybrids and to choose testers and inbreeding materials. Hybrid mules have greater size, more endurance and stress tolerance, longer work life, and survive on poorer nutrition than their parents. Mules do not overeat (founder) or overwork to exhaustion as horses do. Mules have a more acute sense of self-preservation (Clutton-Brock, 1992).

Hybrid Corn Prototype

Farmers associated *hybrid* corn with *hybrid* mules. Dr. W.J. Beal, the first American scientist to breed corn, referred to his variety crosses as mule corns. Iowa State College breeders named a Reid Yellow Dent by Argentine Flint corn cultivar cross *mule corn* (Wallace, 1923). A mule sells for two to three times the price of a horse—a fact useful to hybrid seed–corn salesmen. Farmers cannot reproduce hybrid corns or hybrid mules—neither one self perpetuates. To take advantage of hybrid vigor, new hybrid seed corn must be bought each year and mule colts must be bought from mule breeders. Farmers viewed mules' vigor and longer life as expected advantages of hybrid corn. The record-setting, hot dry summers of 1934 and 1936 were telling years for hybrid corn. A majority of corn fields in Corn Belt states died prematurely from the heat and drought (Troyer, 1983). The nearly unanimous feedback was that the hybrid corns died last. Subsequent acreage of hybrid corn increased dramatically.

How did mules evolve? Six distinct species of living *Equus* (true horses, *E. caballus* L.; onagers, *E. hemoinus* Stehlin; true asses, *E. asinus* Gray; and three species of zebras, *E. quagga* Shortridge, *E. zebra* Heller, and *E. grevyi* Heller) are the results of speciation. In about the beginning of the Pleistocene, the ancestors of these species all belonged to a single, variable interbreeding group. This group spread widely over Asia, Europe, and Africa; and as it did so, the different local populations changed in somewhat different ways. Eventually some of these populations ceased to interbreed with each other and they developed more constant and distinctive differences and became different species. Geographic separation was the isolating mechanism that stopped interbreeding. Each of the lines of descent in the Equidae from Eocene to Recent is a good example of phyletic (direct, without branching) evolution (Simpson, 1951).

Rosetta Stone

Hybrid mules and hinnies can help hybrid corn breeders better understand adaptedness and heterosis in hybrid corn. Wild horses were native north of the

mountains in Europe, Asian asses (donkeys) were native from Asia Minor to the Gobi Desert, African asses (donkeys) were native in northern Africa, and zebras were native in southeastern Africa in the Late Pleistocene. All species of the genus *Equus* can be crossed to produce vigorous hybrids. Reciprocal species crosses differ, probably due to maternal inheritance of mitochondrial DNA or to genomic imprinting (Short, 1997). Female body size is dominant. A mule has the body of a horse with the extremities (head, feet, and tail) of a donkey. A mule, like a donkey, can see all four feet while facing forward, but a horse facing forward can see only its front two feet because of head shape (Chandley, 1989).

In hybrids among Equidae in Europe and Africa, native female hybrids are always superior to the reciprocal cross (Zeuner, 1963). Adaptedness favors larger bodied animals in the cooler climates of northern Europe (>40° N lat) and favors smaller bodied animals in warmer Africa (<35° S lat). A timeworn axiom states no small animals exist in the earth's polar areas because large surface-to-volume ratios cause them to freeze. Larger body size per se may better adapt horses and mules to colder areas nearer the Arctic, and smaller body size may better adapt donkeys and hinnies to hotter areas nearer the equator. Adaptedness delineates superiority over and above heterosis in Equidae hybrids in Europe and Africa. I suggest adaptedness delineates superiority (higher yield) over and above heterosis in U.S. hybrid corn.

Summary

Adaptedness has been critical to the increases in U.S. average corn yields and annual production. Natural and artificial (human) selection improved races and cultivars of corn to better fit their environments. Corn's journeys across 30 degrees of northern latitudes of geography during several thousand years of history explain the development of races and varieties of corn. Darwin's (1859, 1868) principles of natural selection for adaptation explain race formation on the trips from Mexico and explain open-pollinated cultivar development to fit all the environmental niches in the USA. Evolution (natural and human selection) caused the genetic changes, which are determined by inference from historical narrative (Mayr, 1997). Some varieties were better adapted, more popular, and more widely grown. Nature and corn breeders were adapting a tropical crop to a temperate climate.

The first corn hybrids were somewhat more widely adapted than most varieties (Troyer, 1996). Natural selection selects for geographic adaptedness. An inbred from a cultivar adapted to one area crossed with an inbred from a cultivar adapted to another area might produce a hybrid adapted to both areas. In 1936, 96 different open-pollinated cultivars were the parents of 367 different surviving, outstanding inbreds, of which only 36 (10%) were from the five most popular, widely adapted cultivars (Jenkins, 1936). Many breeders of inbred lines wanted local adaptation, which had been important for open-pollinated cultivars. Some breeders chose rare

(unpopular) cultivars; hoping in vain for higher percentage of heterosis. In spite of being greatly outnumbered initially, germplasm from the five most popular, widely adapted open-pollinated cultivars persisted and eventually prevailed (Troyer, 1999, 2004a).

Newer, improved higher yielding hybrids are better adapted to longer daylengths, cooler minimum temperatures, droughts, shorter seasons, and improved crop production practices. At present, five century-old, popular, widely grown open-pollinated cultivars account for 87% of the documented background of U.S. hybrid corn: Reid Yellow Dent, 51%; Minnesota 13, 13%; Lancaster Sure Crop, 13%; Northwestern Dent, 5%; and Leaming Corn, 5% (Troyer, 2004a). This has occurred because farmers want widely adapted hybrids that are more dependable in variable seasonal weather, and because hybrid seed corn companies provide them (Troyer, 1996, 2004a). *Adaptedness was critical; quality of germplasm (better acclimated to their present environment and cultural practices) won out over genetic diversity of germplasm.* United States corn breeders are still adapting a tropical crop to a temperate climate.

When hybrid corn was still quite new, geneticists realized that heterozygosis (degree of heterozygosity) explained both the vigor of the F1 hybrid, which is very heterozygous, and the increased inbreeding depression of inbreds as they became more homozygous (East and Hayes, 1912). Natural selection in corn has favored vigorous plants with heterozygous loci that evolved because of cross-pollinated plants being more vigorous than self-pollinated plants (Darwin, 1875). The first inbreds were very poor for agronomic traits and were difficult to improve. Linkage, many heredity factors, and poor adaptation caused slow progress (Keeble and Pellew, 1910; Jones, 1917; Collins, 1921). Wide area testing and modern information management effectively identified widely adapted hybrids (Bradley et al., 1988). Breeding for more widely adapted hybrids caused more widely adapted open-pollinated cultivars to become prominent in hybrid backgrounds (Troyer, 1999, 2004a). Within-inbred, favorable epistasis is the cause of single-cross hybrid yield superiority (Sharp, 1934; Stringfield, 1950; Weatherspoon, 1970). Higher yielding inbred parents and higher yielding hybrids were good for business. Additive, dominance, and epistatic gene action were exploited. Human selection criteria led to more vigorous, higher yielding, homozygous inbreds.

Natural selection and artificial (human) selection acts on variation caused by mutation and by recombinant gene effects. Mutations increase heterozygosis and meiotic recombination improves epistasis. Heterosis in corn is necessarily complex because of the many genetic differences for morphological traits (more than 40) between Northern Flints and Southern Dents (Table 1). Heterosis is predictable only among closely related corn inbreds; for example, sister homozygous inbreds developed from the same S3 (~87.5% homozygous) row will have the same heterotic group and patterns (AFT, personal experience). By contrast, Kansas hybrid K2234, outstanding in performance over a period of years, involved four inbreds from Pride of Saline open-pollinated

cultivar (Jugenheimer, 1976). The larger mule and the smaller hinny are simpler, more apparent examples of heterosis in hybrids where superiority appears to depend on adaptedness to climate temperature based on body size.

The relative importance of adaptedness and heterosis for yield gain in the first 60 yr of hybrid corn can be examined in Table 3 (or see Duvick, 1999). Heterosis per se gain was 1414.5 kg ha^{-1} or 36% of hybrid gain. Homozygous parent inbreds (no heterosis) gain was 2479 kg ha^{-1} or 64% of hybrid gain. Nonheterotic yield gains were nearly twice heterotic yield gains. I suggest genetic improvements for adaptedness to their environment and to their cultural practices were the major factor in the yield gains of parent inbreds and their hybrids.

Conclusions

1. Darwin's principle of natural selection for adaptation explains formation of Northern Flint and Southern Dent races by isolation and selection, proliferation of open-pollinated cultivars during American westward expansion by adaptation to new environmental niches, and formation of more widely adapted hybrids by selection over time of more widely adapted open-pollinated cultivar backgrounds.

2. Anderson and Brown's (1952) explanation of the origin of Corn Belt Dent from crossbreeding Northern Flint and Southern Dent races, determination that heterosis of Corn Belt maize seems to be due to the mingling of Northern Flints and Southern Dents, and prognostication that degree of difference for morphological traits among parents predicts heterosis remain convincing. No better theories to the contrary have been offered. Anderson's (1944) observation that much of the corn being grown in the USA traces back to Reid Yellow Dent and Lancaster Sure Crop cultivars remains accurate.

3. Genetic gains in grain yield are greater for adaptedness to the conditions of life than for heterosis per se in the U.S. corn yield and production increases since hybrid corn. The relative constancy of percentage of heterosis for yield in adapted, successful corn hybrids occurs because the hybrid and its inbred parents are affected by the season in like manner due to their mutual adaptedness.

4. Heterosis is partially caused by many heterozygous loci of different alleles resulting from adaptation to different conditions of life over time (natural selection). Higher yielding hybrids and higher yielding homozygous inbreds have been simultaneously developed by human selection for favorable additive, dominant, and epistatic genes. Heterotic groups are formed by isolation and selection for adaptedness over time. Heterotic patterns are determined empirically—genetic diversity helps.

5. Single cross hybrids with two complete parent inbred chromosome complements in each hybrid

plant yield more than more complicated hybrids with other things equal. This within-inbred, favorable epistasis has increased yield of inbred parents and their hybrids over time.

6. The objective of U.S. corn breeding has been and still is to adapt a tropical crop to a temperate climate.

Practice proves more than theory.–Abraham Lincoln (Humes, 1996)

Dedication

This paper is dedicated to the memory of Dr. Robert W. Allard, a lifelong, fervent student of adaptedness in plants. He was author of many scientific papers and of an excellent plant breeding text. I enjoyed long talks with him and participating in some of his symposia. He was as stimulating as a breath of fresh air and a good friend.

REFERENCES

Allard, R.W. 1988. Genetic changes associated with adaptedness in cultivated plants and their wild progenitors. J. Hered. 81:1–16.

Allard, R.W. 1997. Genetic basis of the evolution of adaptedness in plants. p. 1–11. In P.M.A. Tigerstedt (ed.) Adaptation in plant breeding. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Allard, R.W. 1999. History of plant population genetics. Annu. Rev. Genet. 33:1–37.

Anderson, E. 1944. Sources of hybrid maize germplasm. Ann. Mo. Bot. Garden 31:357–361.

Anderson, E., and W.L. Brown. 1952. Origin of Corn Belt maize and its genetic significance. p. 124–148. In J.W. Gowen (ed.) Heterosis. Iowa State Press. Ames, IA.

Armstead, I., C. Jiang, M. Hayward, H.R. Lafitte, G.O. Edmeades, D. Hoisington, and J.A. Deutsch. 1997. Genetic analysis of adaptation differences between highland and lowland tropical maize. p. 30–31. In CIMMYT. 1997. Book of Abstracts. The Genetics and Exploitation of Heterosis in Crops, an Int. Symp., Mexico City. 17–22 Aug. 1997. CIMMYT, Mexico D.F., Mexico.

Baker, R.F. 1984. Some of the open-pollinated cultivars that contributed the most to modern hybrid corn. p. 1–19. In J.W. Dudley (ed.) Proc. 20th Annual Illinois Corn Breeders School, Champaign, IL. 6–8 Mar. 1984. Univ. of Illinois, Urbana, IL.

Bowman, M.L., and B.W. Crossley. 1911. Corn. 2nd ed. Waterloo Publishing Co., Waterloo, IA.

Bradley, J.P., K.H. Knittle, and A.F. Troyer. 1988. Statistical methods in seed corn product selection. J. Prod. Agric. 1:34–38.

Brown, W.L., and E. Anderson. 1947. The northern flint corns. Ann. Mo. Bot. Gard. 34:1–34.

Brown, W.L., and E. Anderson. 1948. The southern dent corns. Ann. Mo. Bot. Gard. 35:255–268.

Browne, P.A. 1837. An essay on Indian corn. J. Thompson, Philadelphia.

Chandley, A.C. 1989. Why don't the mule and hinney look alike. Q. J. Brit. Mule Soc. 43:7–10.

CIMMYT. 1997. Book of abstracts. The genetics and exploitation of heterosis in crops. An International Symposium, Mexico City. 17–22 Aug. 1997. CIMMYT, Mexico, D.F., Mexico.

Clutton-Brock, J. 1992. A history of the horse and the donkey in human societies. Harvard Univ. Press, Cambridge, MA.

Collins, G.N. 1921. Dominance and the vigor of first generation hybrids. Am. Nat. 55:116–133.

Crabb, A.R. 1948. The hybrid-corn makers: Prophets of plenty. Rutgers Univ. Press, New Brunswick, NJ.

Crow, J.F. 1948. Alternative hypotheses of hybrid vigor. Genetics 33:477–487.

Crow, J.F. 1952. Dominance and overdominance. p. 282–297. In J.W. Gowen (ed.) Heterosis. Iowa State Press, Ames, IA.

Crow, J.F. 1997. Dominance and overdominance. p. 10. In CIMMYT. Book of abstracts. The Genetics and Exploitation of Heterosis in Crops. An International Symposium, Mexico City. 17–22 Aug. 1997. CIMMYT, Mexico, D.F., Mexico.

Crow, J.F. 1999. Dominance and overdominance. p. 49–58. In J.G. Coors and S. Pandey (ed.) The genetics and exploitation of heterosis in crops. ASA and CSSA, Madison, WI.

Crow, J.F. 2000. The rise and fall of overdominance. p. 225–257. In Jules Janick (ed.) Plant breeding reviews. Vol. 17. John Wiley & Sons, Hoboken, N.J.

Darwin, C.R. 1856–1858. Comparison of nature's selection with man's selection. p. 223–226. In R.C. Stauffer (ed.) Charles Darwin's Natural Selection—Being the second part of his big species book written from 1856 to 1858. Cambridge Univ. Press, New York.

Darwin, C.R. 1859. The origin of species. John Murray, London.

Darwin, C.R. 1868. Variation of plants and animals under domestication. John Murray, London.

Darwin, C.R. 1875. The effects of cross and self fertilization in the vegetable kingdom. John Murray, London.

Davis, R.L. 1929. Report of the plant breeder. Porto Rico AES Annu. Rep. 1927:14–15.

Duddleston, B.H. 1918. Relation of stalk and ear characters to yield. M.S. thesis. Iowa State Univ., Ames, IA.

Dungan, G.H. 1935. Illinois corn performance tests: Results for 1934. Ill. AES Bull. 411:53–88.

Duvick, D.N. 1997. Heterosis: Feeding people and protecting natural resources. p. 6–9. In CIMMYT. Book of Abstracts. The Genetics and Exploitation of Heterosis in Crops. An International Symposium, Mexico City. 17–22 Aug. 1997. CIMMYT, Mexico, D.F., Mexico.

Duvick, D.N. 1999. Heterosis: Feeding people and protecting natural resources. p. 19–29. In J.G. Coors and S. Pandey (ed.) The Genetics and Exploitation of Heterosis in Crops. ASA, Madison, WI.

East, E.M., and H.K. Hayes. 1912. Heterozygosis in evolution and in plant breeding. USDA Bull. 243.

East, E.M., and D.F. Jones. 1919. Inbreeding and outbreeding. J. Lippincott Co., Philadelphia.

Encyclopedia Britannica. 1983. Charles Darwin. William Benton Publ., Chicago.

Goodman, M.M. 1988. The history and evolution of maize. Crit. Rev. Plant Sci. 7:197–201.

Hageman, R.H., E.R. Leng, and J.W. Dudley. 1967. A biochemical approach to corn breeding. p. 45–86. In A.G. Norman (ed.) Advances in agronomy. Vol. 19. Academic Press, New York.

Hallauer, A.R. 2002. Integration of germplasm improvement with corn at Iowa State. p. 11–41. In J.W. Dudley (ed.) 38th Annu. Illinois Corn Breeders' School, Urbana, IL. 4–5 Mar. 2002. Univ. of Illinois. Urbana, IL.

Hallauer, A.R., and J.B. Miranda. 1981. Quantitative genetics in maize breeding. Iowa State Univ. Press, Ames, IA.

Hallauer, A.R., W.A. Russell, and K.R. Lamkey. 1988. Corn breeding. p. 469–564. In G.F. Sprague and J.W. Dudley (ed.) Corn and corn improvement. ASA, Madison, WI.

Hallauer, A.R., W.A. Russell, and O.S. Smith. 1983. Quantitative analysis of Iowa stiff stalk synthetic. p. 34–39. In J.P. Gustafsen (ed.) 15th Stadler Genetic Symposium, Univ. of Missouri, Columbia. AES, Columbia, MO.

Hallauer, A.R., and T.R. Williams. 2000. Genetic diversity among maize hybrids. Maydica 45:163–171.

Hayes, H.K., and R.J. Garber. 1921. Breeding crop plants. McGraw-Hill Book Co., Inc., London.

Hayes, H.K., and F.R. Immer. 1942. Methods of Plant Breeding. McGraw-Hill Book Company, Inc., New York and London.

Hayes, H.K., and I.J. Johnson. 1939. The breeding of improved selfed lines of corn. J. Am. Soc. Agron. 31:710–724.

Hershey, N. 1989. Descendents of John Eby Hershey and Anna Mellinger Hershey. Sutter House, Lititz, PA.

Hinze, L.L., and K.R. Lamkey. 2003. Absence of epistasis for grain yield in elite maize hybrids. Crop Sci. 43:46–56.

Hopkins, C.G. 1913. The Illinois system of permanent fertility. Ill. AES Circ. 167.

Hudson, J.C. 1994. Making the Corn Belt. Indiana Univ. Press, Bloomington, IN.

Hull, F.H. 1945. Recurrent selection for specific combining ability in corn. J. Am. Soc. Agron. 37:134–145.

Hull, F.H. 1952. Recurrent selection and heterosis. p. 451–473. In J. W. Gowen (ed.) Heterosis. Iowa State Press, Ames, IA.

Humes, J.C. 1996. The Wit and Wisdom of Abraham Lincoln. Gramercy Books, New York.

Jenkins, M.T. 1929. Correlation studies with inbred and cross-bred strains of maize. J. Agric. Res. 39:677–721.

Jenkins, M.T. 1936. Corn improvement. p. 455–522. In E.S. Bressman (ed.) Yearbook of agriculture. USDA, Washington, DC.

Jenkins, M.T. 1978. Maize breeding during the development and early years of hybrid maize. p. 13–28. In D.B. Walden (ed.) Maize breeding & genetics. John Wiley & Sons, New York.

Jones, D.F. 1917. Dominance of linked factors as a means of accounting for heterosis. Genetics 2:466–497.

Jones, D.F. 1927. Double crossed Burr-Leaming seed corn. Conn. Ext. Bull. 108.

Jugenheimer, R.W. 1976. Corn improvement, seed production, and uses. John Wiley & Sons, New York.

Jugenheimer, R.W., and A.F. Troyer. 1955. Experimental corn hybrids tested in 1955. Ill. AES Bull. 597.

Keeble, F., and C. Pellew. 1910. The mode of inheritance of stature and time of flowering in peas. J. Genet. 1:47–56.

King, R.C. 1972. A dictionary of genetics. 2nd ed. Oxford Univ. Press, London and Toronto.

Knight, R.L. 1948. Dictionary of genetics. Chronica Botanica Co., Waltham, MA.

Labate, J.A., K.R. Lamkey, S.E. Mitchell, S. Kresovich, H. Sullivan, and J.S.C. Smith. 2003. Molecular and historical aspects of corn belt diversity. Crop Sci. 43:80–91.

Lamkey, K.R., and J.W. Edwards. 2004. Breeding plants and heterosis. p. 189–192. In Robert M. Goodman (ed.) Encyclopedia of plant and crop science. Marcel Decker, New York.

Lamkey, K.R., B.J. Schnicker, and A.L. Melchinger. 1995. Epistasis in an elite maize hybrid and choice of generation for inbred line development. Crop Sci. 35:1272–1281.

Lang, A.L., J.W. Pendleton, and G.H. Dungan. 1956. Influence of population and nitrogen levels on yield and protein and oil contents of nine corn hybrids. Agron. J. 48:284–289.

Leng, E.R., and D.E. Finley. 1956. Illinois corn tests, cultivar performance. Ill. AES Bull. 605:1–32.

Leng, E.R., and G.L. Ross. 1962. 1961 Performance of commercial corn hybrids in Illinois. Ill. AES Bull. 682:1–47.

Lorain, J. 1813. Observations on Indian corn and potatoes. Philadelphia Soc. for Promoting Agric., Memoirs 3:303–325.

Mangelsdorf, P.C. 1974. Corn, its origin, evolution, and improvement. Harvard Univ. Press, Cambridge, MA.

Mayr, E. 1997. This is biology: The science of the living world. Harvard Univ. Press, Cambridge, MA.

Moll, R.H., J.H. Lonquist, J.V. Fortuno, and E.C. Johnson. 1965. The relationship of heterosis and genetic divergence in maize. Genetics 52:139–144.

Moll, R.H., W.S. Salhuana, and H.F. Robinson. 1962. Heterosis and genetic diversity in cultivar crosses of maize. Crop Sci. 2(3):197–198.

Mooers, C.A. 1910. Stand and soil fertility as factors in the testing of cultivars of corn. Tenn. AES Bull. 89:49–60.

Mooers, C.A. 1920. Planting rates and spacing for corn under southern conditions. Agron. J. 12:1–22.

Montgomery, E.G. 1916. The corn crops. Macmillan, New York.

Morrow, G.E., and F.D. Gardner. 1893. Field experiments with corn, 1892. Ill. AES Bull. 25:179–180.

Morrow, G.E., and F.D. Gardner. 1894. Field experiments with corn, 1893. Ill. AES Bull. 31:359–360.

Phillips, R.L. 1999. Research needs in heterosis. p. 501–508. In J.G. Coors and S. Pandey (ed.) The genetics and exploitation of heterosis in crops. ASA, Madison, WI.

Rice, V.A. 1942. Breeding and improvement of farm animals. McGraw-Hill Book Co., New York and London.

Richey, F.D. 1924. Effects of selection on the yield of a cross between cultivars of corn. USDA Bull. 1209.

Richey, F.D. 1945. Isolating better foundation inbreds for use in corn hybrids. Genetics 30:455–471.

Richey, F.D., and L.S. Mayer. 1925. The productiveness of successive generations of self-fertilized lines of corn and crosses between them. USDA Bull. 1354.

Russell, W.A. 1991. Genetic improvement of maize yields. Adv. Agron. 46:245–298.

Saleem, M., A. Aziz, and N. Hussain. 1997. Heterosis in maize hybrids developed from subtropically adapted inbred lines. p. 308–309. In Book of abstracts. The genetics and exploitation of heterosis in crops. CIMMYT, Mexico D.F., Mexico.

Shamel, A.D. 1907. The art of seed selection and breeding. p. 221–236. In G.W. Hill (ed.) Yearbook of agriculture. GPO, Washington, DC.

Sharp, L.W. 1934. Meiosis. p. 250–283. In Introduction to cytology. 3rd ed. McGraw-Hill, New York.

Sheppard, P.M. 1969. Natural selection and heredity. Hutchinson & Co., London.

Shoesmith, V.M. 1910. The study of corn. Orange Judd Co., New York.

Short, R.V. 1997. An introduction to mammalian interspecific hybrids. J. Hered. 88:355–357.

Shull, G.H. 1908. The composition of a field of maize. Am. Breed. Assoc. 4:296–301.

Shull, G.H. 1948. What is heterosis? Genetics 33:439–454.

Simmonds, N.W. 1979. Principles of crop improvement. Longman Group Ltd., London.

Simpson, G.G. 1951. Horses. Oxford Univ. Press, New York.

Sinnott, E.W., and L.C. Dunn. 1939. Principles of genetics. 3rd ed. McGraw-Hill Book Co., New York and London.

Smith, O.S. 1997. Prediction of single cross performance. p. 175. In Book of abstracts. The genetics and exploitation of heterosis in crops. CIMMYT, Mexico, D.F., Mexico.

Smith, O.S. 1998. Trend analysis of U.S. maize yields from 1950 to 1994. Regression model based on agronomic inputs, weather, and genetic trend. ASTA Corn Sorghum Res. Conf. 53:170–179.

Sprague, G.F., and L.A. Tatum. 1942. General vs. specific combining ability in single-crosses of corn. Agron. J. 34:923–932.

Stringfield, G.H. 1950. Heterozygosis and hybrid vigor in maize. Agron. J. 42:145–152.

Sturtevant, E.L. 1899. Cultivars of corn. USDA Off. Exp. Sta. Bul. 57:1–108.

Telleen, M. 1977. The draft horse primer. Rodale Press, Emmaus, PA.

Troyer, A.F. 1983. Breeding corn for heat and drought tolerance. p. 128–143. In D. Wilkinson and R. Brown (ed.) 38th Annual Corn and Sorghum Res. Conf., Chicago. 7–8 Dec. 1983. Am. Seed Trade Assoc., Washington, DC.

Troyer, A.F. 1990. A retrospective view of corn genetic resources. J. Hered. 81:17–24.

Troyer, A.F. 1994. Breeding early corn. p. 341–396. In A.R. Hallauer (ed.) Specialty corns. CRC Press, Boca Raton, FL.

Troyer, A.F. 1996. Breeding widely adapted, popular maize hybrids. Euphytica 92:163–174.

Troyer, A.F. 1999. Background of U.S. hybrid corn. Crop Sci. 39:601–626.

Troyer, A.F. 2000. Temperate corn—Background, behavior, and breeding. p. 393–466. In A.R. Hallauer (ed.) Specialty corns. 2nd ed. CRC Press, Boca Raton, FL.

Troyer, A.F. 2003. Champaign County, Illinois and the origin of hybrid corn. p. 41–59. In Jules Janick (ed.) Plant breeding reviews (Part 1). John Wiley & Sons Inc., Hoboken, NJ.

Troyer, A.F. 2004a. Background of U.S. hybrid corn: II. Breeding, climate, and food. Crop Sci. 44:370–380.

Troyer, A.F. 2004b. Persistent and popular corn germplasm in 70 centuries of evolution. p. 133–231. In C.W. Smith (ed.) Corn: Origin, history, technology, and production. John Wiley & Sons, Hoboken, NJ.

Troyer, A.F. 2004c. Breeding widely adapted cultivars: Examples from maize. In R.M. Goodman (ed.) Encyclopedia of plant and crop science. Marcel Decker, New York.

Troyer, A.F. 2004d. Glen H. Stringfield—Great corn breeder. Maydica 49:147–153.

Troyer, A.F., S.J. Openshaw, and K.H. Knittle. 1988. Measurement of genetic diversity among popular commercial corn hybrids. Crop Sci. 28:481–485.

Troyer, A.F., and R.W. Rosenbrook. 1983. Utility of higher plant densities for corn performance testing. Crop Sci. 23:863–867.

Tuberosa, R., and R.L. Phillips. 2002. Progress in map-based cloning of *Vgt1*, a QTL controlling flowering time in corn. *In* S. Nicolas (ed.) Proc. 57th Annual Corn and Sorghum Res. Conf., Chicago. 11–12 Dec. 2002. Am. Seed Trade Assoc., Washington, DC.

UN/FAO. 2002. Annual crop production estimate. United Nations. Food and Agricultural Organization. Dep. of Statistics. Rome, Italy.

USDA-NASS. 2004a. Illinois farm report. Vol.25, No.15. USDA, Washington, DC.

USDA-NASS. 2004b. Illinois farm report. Vol.25, No.16. USDA, Washington, DC.

USDA-NASS. 2005. Annual crop production estimate. USDA-NASS, Washington, DC.

Vladutu, C., J. McLaughlin, and R.L. Phillips. 1999. Fine mapping and characterization of linked quantitative trait loci involved in the transition of the maize apical meristem from vegetative to generative structures. Genetics 153:993–1007.

Wallace, H.A. 1923. 1923. Mule corn. Wallaces' Farmer 20:627.

Wallace, H.A. 1955. Public and private contributions to hybrid corn—Past and future. p. 107–115. *In* W. Heckendorn and J. Gregory (ed.) Proc. 10th Annu. Hybrid Corn Industry Res. Conf., Chicago. 30 Nov.–1 Dec. 1955. Amer. Seed Trade Assoc., Washington, DC.

Wallace, H.A., and W.L. Brown. 1988. Corn and its early fathers. Rev. ed. Iowa State Univ. Press, Ames, IA.

Weatherspoon, J.H. 1970. Comparative yields of single, three way and double crosses of maize. Crop Sci. 10(2):157–159.

Williams, G.C. 1966. Adaptation and natural selection. Princeton Univ. Press, Princeton, NJ.

Williams, J.O., and S.R. Speelman. 1938. Mule production. USDA Farmers' Bull. 1341. GPO, Washington, DC.

Zeuner, F.E. 1963. A history of domesticated animals. Harper & Row, New York.

Zimmer, C. 2004. Stretching the limits of evolutionary biology. Science (Washington, DC) 34:1235–1236.