

Modern Maize Breeding

Elizabeth A. Lee and William F. Tracy

1 Introduction

Maize breeders during the hybrid era (1939 to present) have been extremely successful in making continuous genetic improvement in commercial grain yield (Fig. 1). Commercial grain yield in the US increased from about 1,300 kg ha⁻¹ in 1939 to 7,800 kg ha⁻¹ in 2005, about 99 kg ha⁻¹ year⁻¹, with similar gains observed in Canada during the hybrid era (80 kg ha⁻¹ year⁻¹) (Lee and Tollenaar 2007). This 6-fold increase in grain yields over a 60 year period is unprecedented among cereals or oil seeds.

The USDA began collecting data on yield in 1862 and from that time maize yields did not change until the 1930s when they began an upward trend which has showed no signs of abating (Tracy et al. 2004). Prior to 1909, nearly all maize breeding was done by farmers or farmer/seedsman, who used mass selection as their main breeding method (Hallauer et al. 1988). Mass selection is a method in which the best ears from the best plants would be selected from a population of maize plants. While this technique has been used since the domestication of plants, it is not very effective for traits with low heritability such as yield. Some farmer/breeders experimented with ear-to-row selection which entails growing and evaluating families derived from individual open-pollinated ears. While this method can be successful in improving traits of low heritability, the lack of knowledge of statistics and experimental design limited the success of this method and yields continued unchanged. Also contributing to static yields were the maize shows that were prevalent during the late 19th and early 20th centuries. In these shows, 10 ears were shown by each exhibitor and those groups that were most uniform and conformed to some ideal type in the mind of the judge were chosen as the winners, with no attention paid to yield or other economic traits. It is likely that the emphasis on uniformity in these competitions contributed to inbreeding and further suppressed any yield

E.A. Lee

University of Guelph, Department of Plant Agriculture, Guelph, ON N1G 2W1 Canada,
lizlee@uoguelph.ca

W.F. Tracy

wftracy@wisc.edu

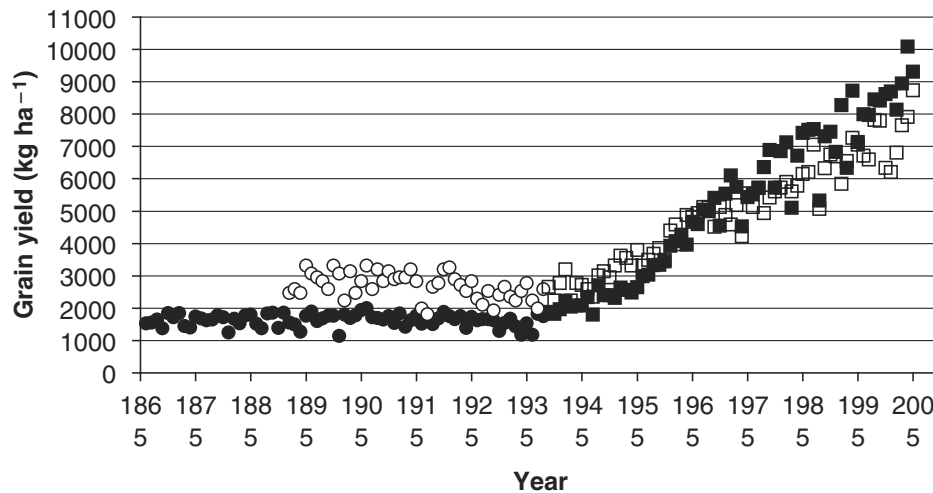


Fig. 1 Average US (1865 to 2005) and Canadian (1892 to 2005) maize yields in kg ha^{-1} (15.5% moisture), 1866 to 1938 (pre-hybrid era; ● – US yields, ○ – Canadian yields), 1939 to 2005 (hybrid era; ■ – US yields, □ – Canadian yields). Data compiled by the USDA and OMAFRA. (From: Lee and Tollenaar 2007)

increases (Hallauer et al. 1988). A third breeding approach attempted during the 19th century was varietal hybridization in which two open-pollinated cultivars would be hybridized and the resulting hybrid would be grown for seed (Beal 1877). Some crosses did reveal reasonable amounts of heterosis (10–15%). But this yield increase was not enough to justify the extra energy and expense of producing the hybrid seed.

Hybrid maize traces its roots back to experiments on heterosis and inbreeding conducted by G.H. Shull (1908, 1909) at Cold Spring Harbor Laboratories in New York and E.M. East (1909) at Connecticut State College. Those observations, made nearly 100 years ago, and methodology outlined by Shull (1909), gave rise to the modern hybrid maize industry (c.f., Crow 1998). Because of the hybrid nature of the crop, modern temperate maize breeding in the US and Canada has evolved into two very distinct activities: inbred line development and hybrid commercialization (Duvick and Cassman 1999; Fig. 2). It is important to understand the distinctions between the two breeding activities, as genetic improvements first must occur within the inbred line development programs before they can be captured and realized in commercial hybrids. Inbred line development is the stage of maize breeding where the greatest amount of *de novo* genetic variation is present, created through recombination giving rise to novel alleles and new allelic combinations. In hybrid commercialization the genetic variation is potentially less, but represented by a far more refined germplasm pool; one that has been through extensive evaluation.

Maize breeding methodologies and philosophies have not remained static during the hybrid era. Breeding philosophies and practices have evolved; incorporating scientific advances in breeding and genetic theory such as early-generation testing (Jenkins 1935; Sprague 1946; El-Lakany and Russell 1971); rapidly adopting improvements in agronomic management practices such as increased plant population densities and modern herbicide chemistries; and recognizing how best to assess the

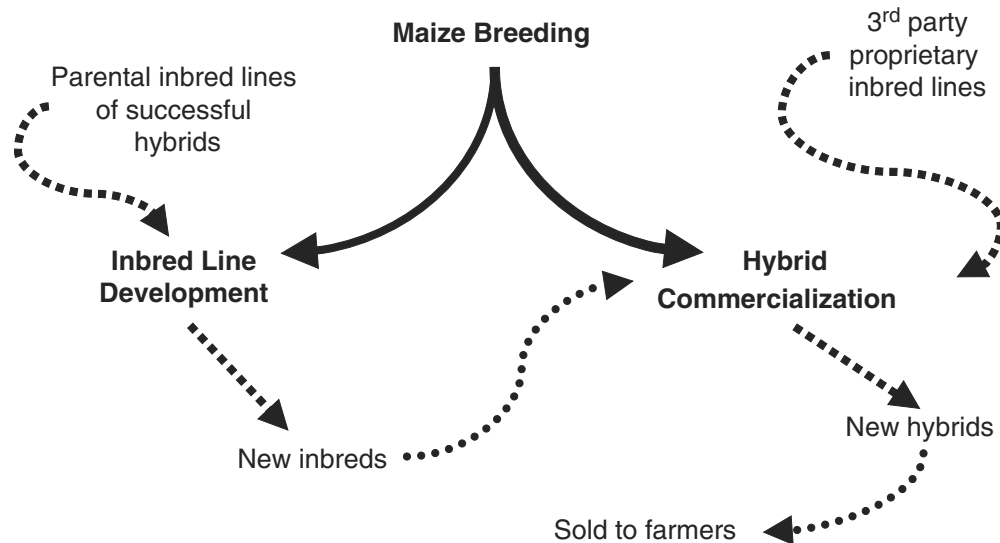


Fig. 2 Overview of a modern maize breeding program. (From: Lee and Tollenaar 2007)

genetic potential of a genotype, through improvements in experimental design and data analysis. Changes such as adoption of improved management practices impacted both inbred line development and hybrid commercialization, while other changes were geared toward one of the two maize breeding activities. Not all that surprising is that most of the innovations in breeding do not affect the generation of genetic material, but rather on how the genetic material is evaluated. The purpose of this chapter is to acquaint the reader with commercial maize breeding in North America circa 2008 – the methodology, the germplasm, and the philosophies.

2 Breeding Objectives

For the vast majority of maize breeding programs in the US and Canada, the primary breeding goals are high yield of machine-harvestable grain and wide adaptation within maturity zones (Troyer 1996). In a sense, these two traits encompass all the genes that determine the fitness of the organism. High yield of machine-harvestable grain indicates the need for alleles that positively affect all the pathways and functions affecting seed production. In addition, the term machine-harvestable indicates that the plant needs to be able to resist stresses that lead to root or stalk lodging or dropped ears. Wide adaptation indicates that the hybrid needs traits that protect yield from abiotic and biotic stresses. For a hybrid to succeed across the Corn Belt within its maturity zone, it must be able to resist the hot dry conditions of the western Corn Belt and the humid conditions which foster many fungal diseases in the east. Increased heterosis is not a breeding objective in the standard commercial maize breeding programs. Heterosis is a measure of the increased performance of a hybrid relative to its parents. Indeed because high seed yields of the inbred parents are so important to the profitability of a hybrid, the ideal hybrid would be very high yielding

with low heterosis. In fact, heterosis of commercial hybrids calculated as a percent of inbred performance has actually decreased over time (Duvick 1984).

In addition to the performance of the hybrid, productivity of the inbreds is important. An inbred that will be used as a seed parent must produce high yields of high quality seed. That is, seed that has good germination and can tolerate mechanical handling and storage without losing vigor. Seed parents must be easy to detassel and have good stalk and root quality so that they can be easily harvested. Pollen parents should produce adequate quantities of viable pollen.

Traditionally, North American corn breeders have focused almost exclusively on harvestable yield and adaptation. However, breeding for specialty markets has increased. Specific goals include specialty starches for food and industrial uses (Boyer and Shannon 2003) and altered cell wall composition for silage and biofuel production (Frey et al. 2004). Sweet corn and pop corn have entirely different uses than corn grown for grain and, while yield remains important, greater attention is given to factors that affect table quality. In sweet corn, immature kernels are consumed, and they consist mainly of endosperm and ovary wall (immature pericarp). Sweet corn quality is determined by the flavor, aroma, and texture of the endosperm and tenderness of the pericarp. Genes affecting ear and kernel appearance are also important (Tracy 2000). Factors that confer high eating quality often result in poor germination and sweet corn breeders must strike a balance between table quality and germination (Marshall and Tracy 2003).

3 Inbreds, Hybrids, and Heterosis

Shull (1908, 1909) and East (1908) laid the theoretical groundwork for the inbred-hybrid breeding method. However, due to the poor performance of first generation inbreds, East and others did not believe this method could be commercially successful. D.F. Jones (1918) overcame this problem with the invention of the double cross hybrid. A double cross is created by making two single cross hybrids ($A \times B$) and ($C \times D$) and then crossing the two single crosses the following season. The seed sold to farmers was from this second cross. The male and female parents in a double cross are vigorous F_1 hybrids and the female parent produces large quantities of high quality seed. This made the production of hybrid seed possible and hybrid corn breeding programs sprang up around the country. However, for the first 30 years of the 20th century, the US agricultural economy was in recession and it was only when New Deal farm policies changed the economy of farming that farmers were willing to invest in increased inputs including hybrid seed. Cycles of inbred and hybrid development resulted in inbreds with improved performance per se. With better inbreds, double cross hybrids gave way to three ways and eventually single crosses in the 1970s. A three way cross uses three inbred lines, $(A \times B) \times C$, while single crosses only contain two, $A \times B$ (Hallauer et al. 1988). Single cross hybrids are the highest yielding and most uniform, and the most common type today in the Corn Belt.

Since Shull's initial papers, there has been debate about the underlying genetic mechanism of heterosis. The two main theories are the dominance theory and the

overdominance theory. The dominance hypothesis attributes heterosis to the accumulation of favorable dominant genes or masking of deleterious recessive alleles in the hybrid (Davenport 1908; Bruce 1910; Keeble and Pellew 1910). In quantitative genetic terms, heterosis results when there is some degree of directional dominance (d) and the parents differ in gene frequency (Bruce 1910; Falconer 1981). The dominance hypothesis can be expressed in terms of a single-locus (B) with no epistasis as

$$\text{Heterosis} = d - \{a + (-a)\}/2 \quad (1)$$

where a and $-a$ are the genotypic values of the parental genotypes (B_1B_1 and B_2B_2) and d is the genotypic value of the non-parental genotype (B_1B_2). The dominance theory is consistent with recent genomic evidence of differences in genic content between maize inbred lines (Fu and Dooner 2002; Song and Messing 2003; Brunner et al. 2005), and has been demonstrated as the underlying mechanism of a heterotic response for grain yield in a quantitative trait locus mapping study (Graham et al. 1997). The other hypothesis, over-dominance, argues that the heterozygous combination of the alleles at a single locus is superior to either of the homozygous combinations (Shull 1908; East 1908). The over-dominance hypothesis, unlike the dominance hypothesis, does not require the presence of either linkage or the involvement of multiple loci for heterosis to be expressed, nor is it necessarily based on classic Mendelian genetics. However, like the dominance hypothesis, it also requires that the parents differ in gene frequency. While there is no direct evidence in support of this hypothesis in the literature, it has not been completely rejected as an underlying genetic cause.

For heterosis to occur the parents must be genetically diverse and therefore the allele frequencies of effective heterotic groups must be divergent. However, a misperception persists on the absolute requirement for the groups to be based on geographical or phylogenetic diversity. Maize breeders in the 1940s created the basis for modern heterotic groups simply by splitting the available inbreds into two groups in an apparently arbitrary way with little attention to phylogeny (Tracy and Chandler 2006). This approach is supported by work by Cress (1967), who suggested that the way to make the most gain in a reciprocal recurrent selection program is to form one pool with the available germplasm and then arbitrarily split the pool into groups. Genetic drift will create an initial divergence of allele frequencies and the selection program will enhance those differences (Cress 1967). Molecular analysis of germplasm in the Pioneer Hi-bred breeding program supports Cress's approach (Duvick et al. 2004). It is clear that well-developed heterotic patterns of mature breeding programs are artificial constructs created by breeders and enhanced by the process of breeding hybrids (Tracy and Chandler 2006).

4 Methods of Inbred Development

While the primary trait of interest is grain yield in hybrid combinations, the inbred lines themselves need to be relatively productive. That is, inbred lines used as “females” in hybrid seed production must produce reasonable amounts of seed with

good germination, and they also must resist lodging. “Male” inbred lines must produce adequate amounts of pollen. There are several methods that can be utilized for inbred line development, which will be outlined below. In general, the methods differ in one of two features, the amount of recombination that is occurring and/or the genome-wide allelic diversity (i.e., number of possible alleles present) of the starting material. Noticeably absent from the methods outlined below is recurrent selection. While recurrent selection has been widely used in the public sector for germplasm improvement, it is not a method that is routinely utilized by the commercial maize breeding sector for inbred line development.

4.1 Pedigree Breeding

Most if not all inbred line development activities in North America use the pedigree method of breeding (Duvick et al. 2004; Mikel and Dudley 2006; Lee and Tollenaar 2007; Fig. 3). Pedigree breeding, as it is structured in the commercial sector, is akin to reciprocal recurrent selection (RRS) (Hallauer and Miranda 1988; Duvick et al. 2004). Breeding crosses tend to be made by crossing inbred lines within a heterotic pattern. Inbred lines from the other heterotic patterns are used to improve the heterotic pattern represented by the breeding cross. This type of breeding scheme (i.e., akin to RRS) allows maize breeders to improve both additive and non-additive genetic

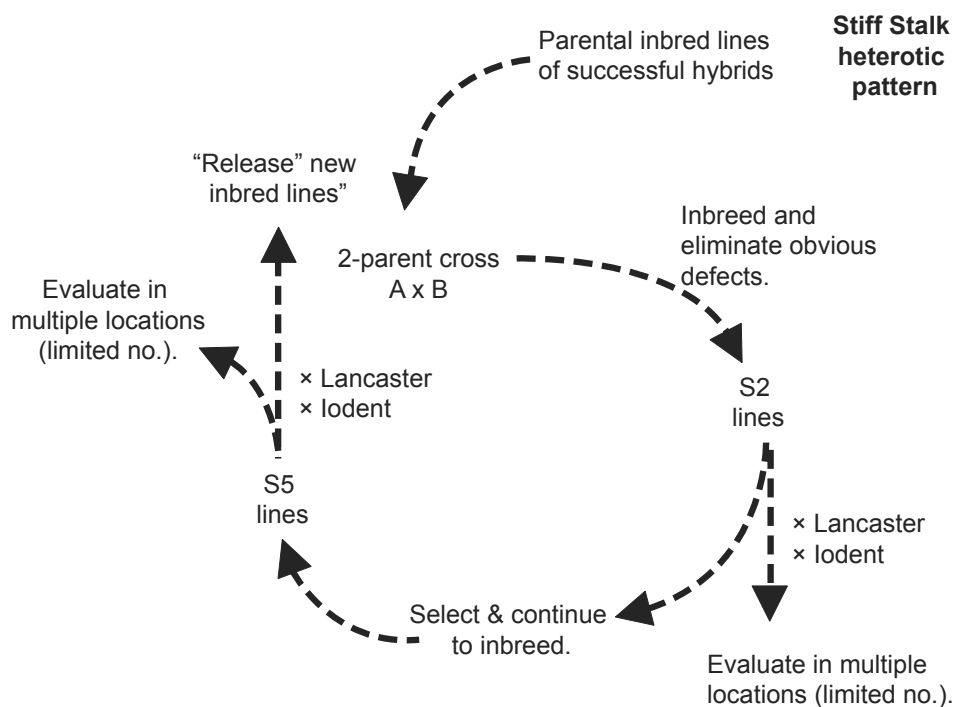


Fig. 3 An example of a typical inbred line development scheme, depicting a 2-parent breeding cross involving two inbred lines from the Stiff Stalk heterotic pattern. (From: Lee and Tollenaar 2007)

effects, resulting in greater overall genetic gains (Comstock et al. 1949). The typical pedigree breeding scheme generally consists of a 2-parent breeding cross within a heterotic pattern. Parent selection is based upon proven commercial utility of the inbred lines. An F_2 population is formed from the breeding cross. Inbreeding is performed for several generations (e.g., S_2) using ear-to-row with each family tracing back to different F_2 plants. During the inbreeding process, genotypes with obvious defects are eliminated. Early generation testing occurs around the S_2 generation, which involves forming topcross hybrids between the S_2 lines and an inbred line from each of the main heterotic patterns. The resulting topcross hybrids are evaluated in a limited number of environments, and selections based on agronomic performance are made. Only S_2 lines that correspond to selected topcross hybrids will be retained in the breeding program. Selected S_2 families are further inbred to the S_5 generation where a second round of topcross hybrid evaluation is performed. Again an inbred line from each of the main heterotic patterns is used to form the topcross hybrids. The hybrids are evaluated in a limited number of environments and selections are based on agronomic performance compared to commercial hybrids (i.e., checks). In general, all testing during inbred line development is done in hybrid combinations, involving a relatively limited number of hybrid combinations, in a relatively limited number of environments, and focused primarily on grain yield. At this stage, any superior inbred lines are then considered for release to the hybrid commercialization side of the breeding activities (Lee and Tollenaar 2007). Marker assisted breeding, a variation of the pedigree method, is used to varying degrees by many companies. Based on the phenotype data from early generation testing, molecular marker genotyping is used in conjunction with off-season nurseries to reduce inbred development time.

4.2 *Dihaploids*

The use of double haploids in breeding has been readily adopted for many homogenous, homozygous crops (e.g., canola, wheat, barley) (reviewed by Forster et al. 2007). The attraction for breeders is that the breeding material essentially moves directly from a segregating population of gametes to a homozygous, heterogeneous collection of plants (cultivars) without the time consuming process of inbreeding. The main characteristic that these crops share is that selection for performance is not practiced in the early generations of inbreeding, due to extremely limited seed quantities severely restricting the amount of field testing that can be carried out. Maize, unlike the crops mentioned above, does not suffer from restricted seed supply for testing early generations. All meaningful testing for grain yield is done in hybrid combinations, leading to essentially unlimited seed quantities from any generation. However, in recent years, there has been a renewed interest in using doubled haploids in maize inbred line development. The apparent attraction is probably a combination of several factors. (1) Reducing the time of the inbreeding process and therefore shortening the time between generations of inbred lines should lead to greater genetic gain per unit time. (2) In the large multinational breeding companies, resource utilization models probably favor separating

the inbred line development process into two distinct activities - the inbreeding process which can be globally centralized in a single facility and the testing process which, due to maturity and environmental differences and genotype-by-environment interactions, still requires numerous regional testing facilities.

Maize haploid plants can be generated through several different means: *in vitro* via microspore (Pescitelli et al. 1989) or anther culture (Genovesi and Collins 1982; Barloy and Beckert 1993), or *in vivo* through the use of inducer lines. There are several inducer lines that have been used to generate maternal (gymnogenetic) haploids. Stock 6 (Coe 1959; Sharkar and Coe 1966), RWS (Röber et al. 2005), KEMS (Deimling et al. 1997), UH400 (MaizeGDB 2007), and KMS and ZMS (Chalyk et al. 1994; Chalyk and Chebotar 2000). Paternal (androgenetic) haploids can be generated using the *indeterminate gametophyte1* (*ig1*) mutation as the inducer (Kermicle 1969; U.S. Patent 5749169). Most double haploids in commercial maize breeding are generated using maternal inducer lines. While the original maternal inducer line, Stock 6, generated haploids at a frequency approaching 3%, the inducer lines used commercially have frequencies of haploid induction approaching 10% (Röber et al. 2005). To generate maternal haploids, the inducer line is used as the pollen donor and generally a visible recessive seedling mutant (e.g., *glossy1*, [*gl1*] or *liguleless2* [*lg2*]) is incorporated into the germplasm from which haploids are being derived. Seed from the cross between the donor germplasm (female parent) and the inducer line (male parent) is grown and screened for seedlings expressing the recessive seedling mutant. Those seedlings that express the seedling mutant are putative haploid plants. Alternatively, an anthocyanin marker system allows F_1 kernels to be screened for putative haploids. The inducer line may be homozygous for all of the functional alleles required for aleurone and embryo face color (e.g., *A1*, *A2*, *C1*, *C2*, and *R1-nj*). The F_1 seed will have colored aleurone and scutellum (i.e., embryo face) but, at a low frequency, colored aleurone and colorless scutellum kernels will appear. Those kernels represent putative haploids (reviewed in Röber et al. 2005). Regardless of the mechanism of haploid generation, chromosome doubling of haploid plants may rely upon spontaneous doubling, or the use of nitrous oxide (Kato 2002) or colchicine (Gayen et al. 1994).

4.3 Backcross Breeding

The goal of most backcrossing programs is to improve a particular strain (recurrent parent) for a specific characteristic, usually a single gene, obtained from a donor parent (Tracy 2004). In most backcross programs, the objective is to recover the recurrent parent essentially unchanged except for the introgression of the new characteristic. Backcrossing allows the plant breeder more precise control of allele frequencies than other traditional plant breeding methods. On average, with each backcross generation (BC) 50% of the recurrent parents alleles are recovered (e.g., F_1 – 50% [recurrent parent alleles]; BC_1 – 75%; BC_2 – 87.5%; BC_3 – 93.25%; etc.). This is the theoretical average. Linkage and epistasis will result in the persistence of

unwanted donor alleles and chromosome segments. Molecular markers can be used to reduce the size of donor linkage blocks and reduce the number of generations of backcrossing needed to recover the recurrent parent's genotype.

Compared to other crops, backcrossing has not been heavily used in maize breeding. Backcrossing has been used to incorporate disease resistance genes into elite inbreds or to transfer inbred nuclear genotypes into male sterile cytoplasms (Hallauer et al. 1988). However, with the widespread use of transgenes in maize breeding, backcrossing has become a standard tool of the maize breeder. Most commercial maize breeding programs have adopted the process of developing new inbreds from non-transgenic germplasm, and then, as new inbreds show promise, they will begin backcrossing in desired transgenes, at the same time maintaining the original non-transgenic inbred. Thus if a particular transgene is removed from the marketplace, or the use agreements are no longer valid, the new inbred is not lost. Also this permits the sale and production of non-transgenic versions of the new hybrids in locations that disallow the use of transgenes.

5 Hybrid Evaluation

As mentioned earlier, commercial maize grain yields during the hybrid era (1939 onward) have increased over 6-fold. This increase is not exclusively due to genetic improvement, as there have been substantial changes to agronomic practices during this 65–70 year period. Starting somewhere in the 1960s, commercial fertilizers were used, with increasing nitrogen levels occurring until the mid-1980s (cf., Troyer 2004; Crosbie et al. 2006). Better weed control was achieved through use of herbicides [e.g., 2,4-D was first used commercially in 1945 and Atrazine® was first used commercially in 1965 (cf., Troyer 2004)]. More uniform distribution of plants within a field was achieved by reducing row widths from 102 cm to 76 cm in the mid-1960s to early-1970s (cf., Troyer 2004). Earlier maize planting (Duvick 1989; Kucharik 2006) has effectively increased the duration of the growing season and, consequently, the period of time that plants can absorb incident solar radiation. Finally, plant population densities gradually increased from 30,000 plant ha⁻¹ to 79,000 plants ha⁻¹ (cf., Crosbie et al. 2006). In general, 60% of the increase in grain yield is attributed to genetic improvement (Duvick 1992) with 40% being attributed to improved agronomic practices (Cardwell 1982). As the agronomic practices changed, breeders incorporated these changes into their testing programs, meaning that, realistically, 100% of the increase in grain yield is actually due to the interaction between genetics and agronomic practices (Tollenaar and Lee 2002).

In contrast to inbred line development, hybrid commercialization generally involves a multi-tiered testing system (Duvick and Cassman 1999). More hybrid combinations are tested in fewer environments during the early testing phase while, in the later testing phases, fewer hybrid combinations are tested in more environments. Again, grain yield is the primary trait of interest. Testing for grain yield is always done in hybrid combinations, and testing is done using the most current agronomic

practices. The specific traits that are assessed are: (1) machine harvestable grain yield adjusted to 15.5% grain moisture (bu ac⁻¹ or Mg ha⁻¹); (2) grain moisture at harvest (%); (3) test weight, a measure of bulk density (lbs bu⁻¹ or kg hl⁻¹); (4) broken stalks, dropped ears, root lodging; (5) days to 50% anthesis, days to 50% silking, and the interval between silking and anthesis; (6) germination under cold, wet conditions (i.e., cold germ test); (7) disease resistance (ear, stalk, and leaf diseases); and (8) general plant appearance.

Grain moisture at harvest is used by many breeders as the best assessment of the “maturity” of a hybrid. “Maturity” is a term that refers to whether a hybrid is adapted to a particular environment. Several systems have been developed to aid breeders and producers to place genotypes into the correct adaptation zones. In N. America, the Minnesota Relative Maturity (RM) system, Growing Degree Days (GDDs), and Ontario Corn Heat Units (OCHUs) are commonly used, while in Europe the Food and Agriculture Organization developed the FAO system (Troyer 2000a) (Table 1). The “ideal” hybrid is one that will maximize the full growing season available (i.e., flower late enough to produce maximal leaf area to intercept incident solar radiation), yet flower early enough that the grain reaches physiological maturity (i.e., black layer formation) before the first killing frost, and facilitate moisture loss from the kernel (i.e., dry down). At physiological maturity, grain moisture is >30% but <40%, while the target grain moisture for machine harvest is ~28% for “high moisture corn” and 15–22% for grain corn. Grain corn with moisture levels >15.5% is dried prior to storage and sale. If it is sold at grain moistures above 15.5%, the sale price will be reduced (i.e., docked), penalizing the producer. Several attributes influence maturity – flowering date, kernel type (flinty vs. floury), and husk characteristics (senescing, loose husks vs. green, tight husks). There is a strong positive linear relationship between flowering date and grain yield, flowering date and grain moisture, and grain moisture and grain yield (Fig. 4). Longer season

Table 1 Maize relative maturity rating systems: RM, GDUs, OCHUs, and FAO. (Adapted from Troyer 2000a)

Minnesota Relative Maturity (days)	U.S. Growing Degree Days (GDUs)	Ontario Corn Heat Units (OCHUs)	FAO (units)
70	1650	2100	100
75	1750	2300	
80	1850	2500	200
85	1950	2600	
90	2050	2700	300
95	2150	2800	
100	2250	2900	400
105	2350	3200	
110	2450	3400	500
115	2550	3500	
120	2650	3700	600
125	2750	3900	
130	2850	4100	700
135	2950	4300	
140	3050	4500	800

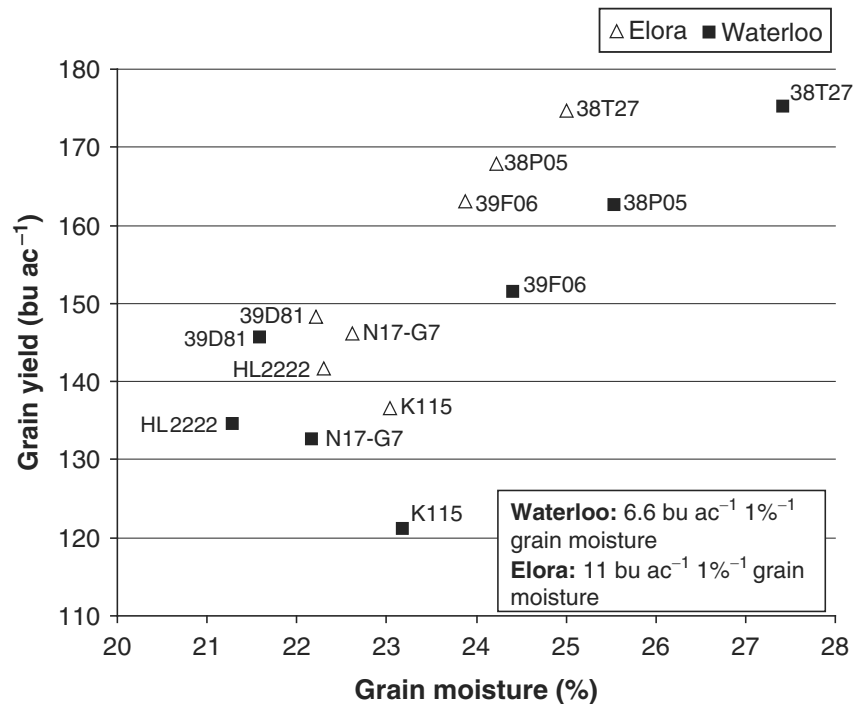


Fig. 4 The yield moisture paradigm in maize. Seven entries, 16 replications at each location, 2 locations, grown in 2002. Maturity ratings for the hybrids are: Pioneer hybrids 38T27 (2900 OCHUs), 38P05 (2850 OCHUs), 39F06 (2650 OCHUs), and 39D81 (2600 OCHUs); Hyland hybrid HL2222 (2450 OCHUs); Syngenta hybrid N17-G7 (2600 OCHUs); Pride hybrid K115 (2450 OCHUs). Accumulated heat units at Elora and Waterloo in 2002 were 2889 and 2750 OCHUs, respectively. Least significant differences (LSD) (0.05) for grain moisture and grain yield are 0.73% and 9.57 bu ac⁻¹, respectively.

hybrids are higher yielding and have higher grain moistures. Depending upon year and location, anywhere from a 6.6 to an 11 bu ac⁻¹ decrease in grain yield for every 1% decrease in grain moisture is not uncommon (Fig. 4). To compensate for the yield-moisture paradigm in selection, many breeders assess hybrids based on their Y/M index, which is a selection index derived by dividing grain yield (adjusted to 15.5% grain moisture) by grain moisture at harvest.

Some of the experimental design and data analysis innovations, while also important for inbred line development, have substantially altered the hybrid commercialization aspect of maize breeding. In the early 1980s in North America, there was a shift in hybrid evaluation procedures. Instead of emphasizing relatively high precision per location at few locations (i.e., many replications, fewer locations), the new procedures emphasized relatively low precision at a large number of locations (i.e., one replication, but more locations) (Bradley et al. 1988). This shift encompassed an increase in the number of locations and years and a change in the type of location. The type of location shifted from high-yielding environments to environments that are most likely to occur in commercial maize production, including stress environments (Bradley et al. 1988). The traditional method of making hybrid comparisons, at that time, involved head-to-head comparisons of the experimental hybrid to various comparison

hybrids grown in the same location and trial (e.g., Bradley et al. 1988; Crosbie et al. 2006). Another shift in evaluation procedures was facilitated by increased computational power and necessitated by the change in focus of the breeding companies' product lines. During the 1980s, several mergers and acquisitions occurred, creating a national or multi-national breeding focus rather than a regional breeding focus to their product lines. While genotype-by-environment interactions ($G \times E$) have always been an impediment to identification of superior genotypes, shifting from breeding for a target population of environments (TPEs) encompassing large geographic areas increases the likelihood that $G \times E$ will confound identification of superior genotypes relative to breeding for regionally-defined TPEs. As an aid in handling $G \times E$, geographic information system (GIS) approaches are now being utilized to define TPEs into environmental classes which, in turn, aids in predicting hybrid performance (Löffler et al. 2005).

6 Germplasm

Maize breeding in North America, unlike breeding activities for many other crop species, has been done primarily in the private sector for the past 30+ years. Movement of this activity out of the public domain has been accompanied by legal protection of the commercial germplasm through legally binding "use agreements", US patents, and the US Plant Variety Protection Act (PVP act). The goal of this section is to give an overview of the commercial North American germplasm circa 2008. The genetic base of the North American hybrid maize industry represents only a small portion of the entire *Zea mays* gene pool. There are 250 to 300 races of maize (Brown and Goodman 1977), of which only one, the Corn Belt Dent, is the predominant source of commercial germplasm (Goodman 1985). Of the hundreds of open-pollinated varieties (OPVs) of Corn Belt Dent that were grown up to the 1940s, only half a dozen or so can be considered as significant contributors to current inbred lines. But the overwhelming majority of the inbred lines trace their pedigree back to only two OPVs, Reid Yellow Dent and to a far lesser extent Lancaster Surecrop (Goodman and Holley 1988; Tracy and Chandler 2006; Troyer 2008).

One of the consequences of the hybrid concept was the development of heterotic patterns, also referred to interchangeably as heterotic groups. These groups were "created" by breeders as a means of maximizing the amount of hybrid vigor and ultimately grain yield in a more predictable manner (reviewed by Tracy and Chandler 2006). Modern hybrids, then, are the result of crossing an inbred line from one heterotic pattern with an inbred line from a different heterotic pattern. Today, inbred lines are classified into heterotic groups and are further sub-divided into families within a heterotic group. Classification of heterotic patterns is generally based upon several criteria such as pedigree, molecular marker-based associations, and performance in hybrid combinations (Smith et al. 1990), and has resulted in somewhere between two and seven distinct heterotic patterns being described (Smith and Smith 1989; Troyer 1999; Lu and Bernardo 2001; Gethi et al. 2002; Mikel and Dudley

2006). We have chosen to represent the germplasm as three main heterotic patterns “Stiff Stalk”, “Lancaster” and “Iodent”, and a miscellaneous category of lines that do not fit into the three primary heterotic patterns in the northern and central US and Canadian corn growing regions (Fig. 5). Most conventional inbred line development has focused on “recycling” (i.e., intermating) lines within a heterotic pattern and even within a family; however at least two novel heterotic patterns have arisen: “Maiz Amargo” and “Commercial Hybrid” derived germplasm (Mikel and Dudley 2006).

In the mid to late 1980s, virtually all commercial North American hybrids could be traced back to six public inbred lines or their close relatives: Lancaster-type inbreds C103, Mo17 and Oh43 and Reid-type lines B37, B73 and A632 (Goodman 1990). A recent US plant patent survey suggests that the current commercial North American maize germplasm pool is essentially based on seven inbred lines (B73, LH82, LH123, PH207, PH595, PHG39, and Mo17) with very little evidence of outside germplasm entering the commercial germplasm pool (Mikel and Dudley 2006). Two of these lines are the public inbreds B73 and Mo17 that were identified by Goodman (1990); however the remaining five are the product of commercial inbred line development activities. Inbred lines LH82 and LH123 were developed by Holden’s Foundation Seeds (now a subsidiary of Monsanto), with LH82 representing a distinct family (referred to as “LH82-type”) from the “Lancaster” heterotic pattern and LH123 representing a distinct family from the “commercial hybrid derived” heterotic pattern. Inbred lines PH207, PH595, and PHG39 were developed by Pioneer Hi-Bred International (now a subsidiary of DuPont). PH207 represents one of the distinct “Iodent” families. PH595 represents a distinct non-Stiff Stalk, non-Iodent

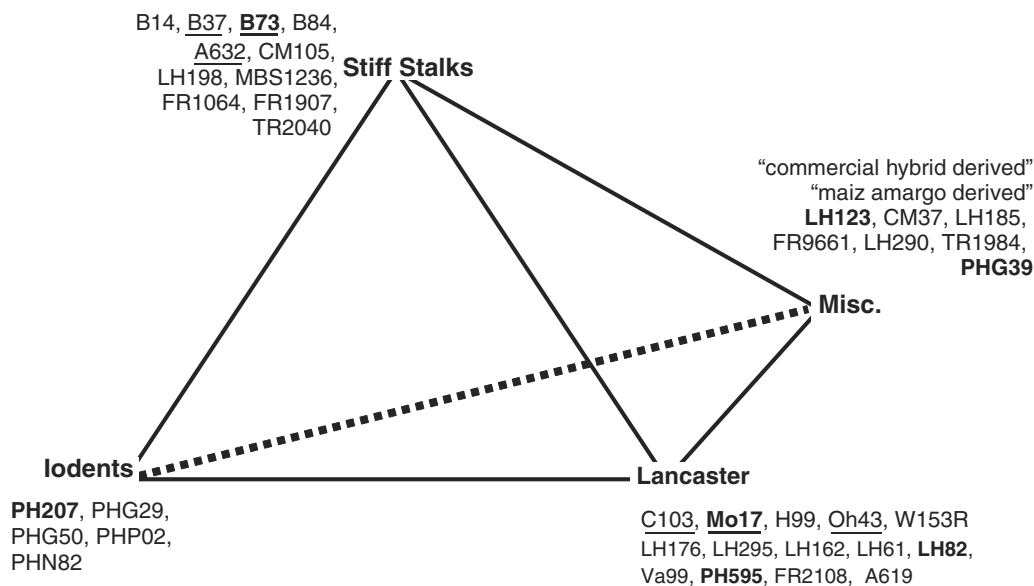


Fig. 5 Northern Corn Belt Dent heterotic patterns. Inbred lines in **bold** are the lines identified by Mikel and Dudley (2006) as those that formed the commercial germplasm pool. Lines under-scored are the public inbred lines identified by Goodman (1990) as being present in virtually all commercial hybrids. (Based on Troyer 1999; Mikel and Dudley 2006; Lee and Tollenaar 2007)

heterotic pattern from Pioneer that is probably best associated with the rather broad “Lancaster” heterotic pattern, through the Oh7-Midland and Oh43 families. The final line, PHG39, represents the “Maiz Amargo” heterotic pattern which traces its origins to the Argentine Maiz Amargo germplasm (Mikel and Dudley 2006).

The pedigree origin of the “Stiff Stalk” heterotic pattern traces back to a 16-line synthetic breeding population developed by George Sprague at Iowa State University in the 1930s, called Iowa Stiff Stalk Synthetic (BSSS) (Sprague 1946; Hallauer et al. 1983). As a group, the 16 parental lines of BSSS were 75% Reid Yellow Dent (Troyer 2000b). The “Iodent” heterotic pattern traces its origins back to an OPV called Iodent and another called Minnesota 13, both of which were selections from the Reid Yellow Dent OPV (reviewed by Troyer 1999; Tracy and Chandler 2006; Mikel and Dudley 2006). The pedigree origin of the “Lancaster” heterotic pattern is probably the most misleading. The name implies that the pattern traces its origins to the OPV Lancaster Surecrop; however, the lines associated with this pattern are mostly Reid Yellow Dent in origin (Tracy and Chandler 2006). The “Lancaster” pattern, as we have chosen to represent it, is quite broad, being grouped into three main families of lines: LH82, C103, and Oh43. Inbred line C103, a parent of Mo17, is the only line that is directly from the Lancaster Surecrop OPV. Oh43 is 50% Lancaster Surecrop OPV by pedigree (Gerdes and Tracy 1993). We have chosen to associate LH82 with the “Lancaster” heterotic group based upon two pieces of evidence. First, even though LH82’s pedigree (610 × LH7; 610 was a selection from W153R which was from the OPV Minnesota 13) does not indicate an association with the Lancaster OPV, molecular marker data suggests that W153R and Oh43 are more closely related to one another than they are to Mo17 and B73 (Gethi et al. 2002). Secondly, and perhaps more importantly, use of LH82 in further generations of inbred line development has involved crosses with other lines associated with Lancaster Surecrop, Oh43 and Oh07-Midland lines (see Figure 2 from Mikel and Dudley 2006).

The commercial germplasm base circa 2008 is almost exclusively from the Corn Belt Dent race of maize, with the Reid Yellow Dent OPV having the greatest contribution. The heterotic patterns that are used to group inbred lines are primarily a means of managing germplasm to exploit heterosis in a more predictable manner, they were created by breeders, and the names may no longer reflect the pedigree origins of the lines associated with the heterotic group. Finally and perhaps most importantly, the heterotic groups are dynamic. The “families” within a pattern evolve over time, the relative importance of a family changes over time, and “novel” heterotic patterns arise over time.

7 Germplasm Enhancement

Germplasm enhancement programs attempt to address the lack of racial diversity in the commercial germplasm base. The goal of most germplasm enhancement programs is to improve the adaptation and performance of non-commercial germplasm, so

that it might be useful to hybrid development programs. In North America, germplasm improvement programs usually involve either introgression of non-Corn Belt Dent germplasm into the commercial germplasm pool, or employ one of a number of recurrent selection methods on Corn Belt Dent germplasm.

7.1 *GEM Program*

Concern about the narrow genetic base underlying the hybrid corn industry has led to programs designed to diversify breeding germplasm. The GEM¹ (Germplasm Enhancement of Maize) program represents one of these efforts. GEM represents a public-private sector collaboration in which elite tropical and sub-tropical germplasm (i.e., from non-Corn Belt Dent races of maize) is crossed to private sector inbred lines. Crosses for the southern US generally contain 50% Corn Belt Dent germplasm, while lines developed for the northern US generally contain 75% Corn Belt Dent germplasm. Inbreds are developed from these crosses following the pedigree method and early generation testing as described above (Carson et al. 2006).

7.2 *Recurrent Selection*

The general goal of recurrent selection programs is to increase the frequency of desirable alleles while maintaining genetic variation in the population (Hallauer and Miranda 1988). In maize breeding, a population is a heterogeneous mixture of heterozygous genotypes derived by intermating inbred lines and/or OPVs. Populations are maintained by randomly intermating individuals in the population or allowing open-pollination under isolation. Recurrent selection programs are cyclic with a cycle consisting of a generation in which selection takes place followed by recombination of the selects. In academic research, the term recurrent selection generally indicates a closed population (i.e., no new germplasm being incorporated) unless otherwise specified. Hallauer and Miranda (1988) and Bernardo (2002) outline numerous recurrent selection programs. Recurrent selection programs are generally divided into either intra-population recurrent selection, in which selection is within one population, or inter-population, in which selection is based on test crosses to unrelated inbreds or populations. Intra-population systems target additive genetic effects, while inter-population programs attempt to select both additive and non-additive genetic effects. Recurrent selection programs can be very simple, such as mass selection, in which a large population of maize plants are grown and the best individuals are selected to supply seed to the following generation, or complex, such as some reciprocal recurrent selection schemes which may take as many as four growing seasons to complete a single cycle.

¹ Additional information on GEM can be found at www.public.iastate.edu/~usda-gem/homepage.html.

Maize is highly plastic and very responsive to selection. The generalized formula for response to selection is

$$R = h^2 S \quad (2)$$

Where R equals the response to selection, h^2 is the narrow sense heritability, and S is the selection differential, which is the difference between the mean performance of the selected individuals and the mean of the parental population (Bernardo 2002). Narrow sense heritability is an estimate of the average effects of the alleles passed from parents to offspring and

$$h^2 = V_A / V_p \quad (7.3)$$

V_A is the variance due to additive effects and V_p is the phenotypic variance.

If h^2 equals 1, then the trait is unaffected by the environment, and $R=S$. However, most quantitatively inherited traits are strongly affected by the environment and, for a traits such as grain yield, h^2 might be in the range of 0.1–0.4. For traits with low heritability, single plant selection or selection of families based on unreplicated evaluation is ineffective. Heritability can be increased by increasing the additive variance relative to the phenotypic variance. This can be done by replicating evaluation plots at a single location or increasing the number of environments in which plots are evaluated. Increasing the selection differential (S) will result in greater gain, but this means that a smaller proportion of the original population will be selected. If too few families are saved, inbreeding and genetic drift will result. A large selection differential and reduced inbreeding can be achieved if large numbers of families are evaluated and at least 15 families are saved for recombination.

Response to selection (R) can also be increased if selection can be made before pollination, such that both the male and female parents (biparental control) can be selected. In this case, gain will be twice as great as for a trait which can only be determined after pollination, such as grain yield, and in which only the female parents are selected and allowed to open-pollinate with the entire population (uniparental control). Schemes have been derived such that biparental control can be used for traits such as a grain yield, but these require an additional growing season that will increase gain per cycle but decrease the gain per season.

7.3 *Divergent Recurrent Selection*

Divergent recurrent selection is a form of recurrent selection in which, starting from an initial closed population, a trait is selected in opposite directions and populations divergent for that trait are developed. Perhaps the best known example is the Illinois high oil/low oil and high protein/low protein long term selection experiment in which there have been more than 100 generations of selection (Dudley and Lambert 2004). There are numerous other examples including root and stalk strength populations at Missouri (Abedon et al. 1999; Flint-Garcia et al. 2003), Iowa ear length populations (Hallauer

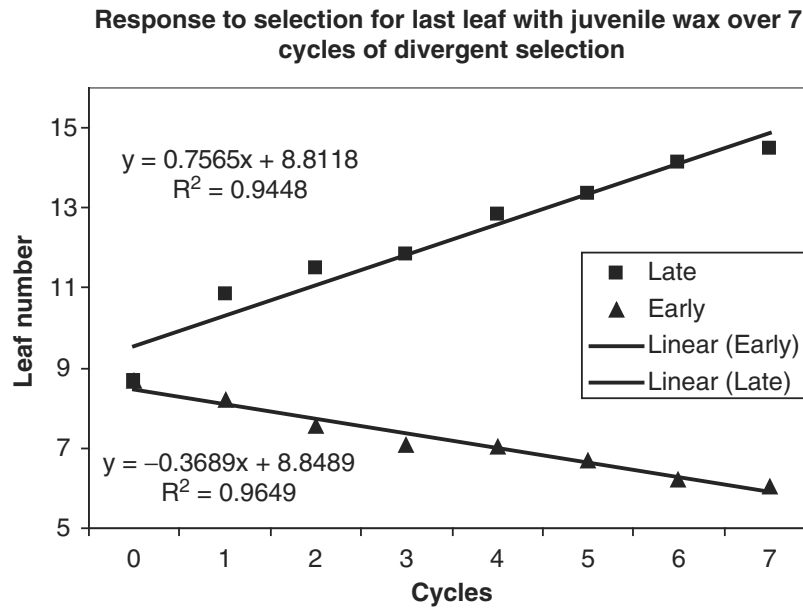


Fig. 6 Direct response to divergent recurrent selection for early and late last leaf with juvenile wax in Minn11 over seven cycles of selection including significant trend lines with corresponding equations and coefficients of determination (R^2). (From: Reideman et al. 2008)

et al. 2004) and endosperm and vegetative phase change populations at Wisconsin (Fig. 6) (Tracy and Chang 2007; Reideman et al. 2008). Divergent recurrent selection experiments can be useful in understanding the limits of selection and also the relationship between the selected trait and unselected traits that change in response to selection. Are such changes due to linkage, pleiotropy, physiological relationships (e.g. source – sink), or an artifact of the selection method? Genomics tools can be applied to divergent populations to determine the underlying genetic and physiological mechanisms between the selected trait and traits indirectly affected by selection.

8 Conclusions

The inbred-hybrid breeding method has been highly effective in increasing maize yields. Average grain yield in the US increased from about 1,300 kg ha⁻¹ in 1939 to 7,800 kg ha⁻¹ in 2005. Increased yields are in part due to improved agronomic practices and increased inputs, but increased yields could not have been realized without genetic improvements. Maize breeders created and continue to create genotypes that respond favorably to modern agronomic practices. During the first 70 to 80 years of the hybrid era, development and application of experimental design and biometry contributed greatly to genetic gain while genetic information was seldom used directly in maize breeding. Today, with genomics tools, plant breeders are able to apply genetic information directly. The combination of genomics, experimental design, biometry, and selection theory will allow maize breeders and maize growers to continue increasing maize productivity well into the 21st century.

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