The Historical and Biological Basis of the Concept of Heterotic Patterns in 'Corn Belt Dent' Maize

W.F. Tracy and M. A. Chandler, Department of Agronomy, College of Agricultural and Life Sciences, University of Wisconsin-Madison.

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Abstract

In 2004 the concept of heterotic patterns is fundamental to maize breeding theory and practice, especially in temperate regions. As the use of hybrids increases in tropical maize and in other crop species, plant breeders apply the lessons of Corn Belt Dent (CBD) heterotic patterns. However, the origin and development of the concept of CBD heterotic patterns have not been critically examined. CBD heterotic patterns were created by breeders, and are <u>not</u> the result of historical or geographical contingencies. While the phenomenon of hybrid vigor (heterosis) and its effects on various traits have been known since the early 1900s, the concept of heterotic patterns developed in the 1960s and 1970s. Academic interest in heterotic patterns increased in the late 1980s, stimulated by the availability of DNA based markers and attempts at using markers to identify heterotic patterns. For CBD open-pollinated varieties and first cycle inbreds it would <u>not</u> have been possible to identify heterotic groups using molecular markers, had markers been available. CBD heterotic patterns were created by breeders through trial and error from a single race of corn. The application of the current concept of heterotic patterns in a hybrid breeding program results in increased divergence between the groups.

In 2004 the concept of heterotic patterns is an integral component of hybrid maize breeding theory and practice. Heterotic patterns simplify germplasm management and organization. Heterotic patterns inform the breeder when choosing parents for crosses for inbred development and inbred testers to evaluate combining ability of newly developed inbreds. Usually there are two groups in a heterotic pattern and there may be subgroups within the two main groups. The current concept of heterotic patterns suggests that the parents of populations for inbred development should come from the same group and testers for newly developed inbreds come from the opposite group.

Melchinger and Gumber (1998) define a heterotic group as "*a group of related or unrelated genotypes from the same or different populations, which display similar combining ability and heterotic response when crossed to genotypes from other genetically distinct heterotic groups*." A heterotic pattern is a specific pair of two heterotic groups.

As the use of hybrid cultivars increases in tropical maize and in other crop species, plant breeders apply the lessons of 'Corn Belt Dent' (CBD) heterotic patterns to those crops. However, the origin and development of the concepts underlying our ideas on CBD heterotic patterns have never been critically examined.

In the 1970s, when I (WFT) first became involved in maize breeding I was told the story of CBD heterotic groups (I'm not sure those exact words were used). I was told of the origin of CBD in which 'Southern Dents' from the southeastern US and 'Northern Flints' from the northeast were carried by pioneers across the Appalachians into the Northwest Territory (lands bordered by the Great Lakes, and the Mississippi and Ohio Rivers). The two races of corn intermated, at first accidentally and then deliberately, by farmers, creating a new maize race, Corn Belt Dent. As part of the story I was told that the most important maize hybrids were made by crossing inbreds derived from the open-pollinated variety (OPV) 'Reid Yellow Dent' (Reid) with inbreds derived from 'Lancaster Surecrop' (Lancaster) another OPV. Perhaps most importantly, I learned that these two facts were connected. Reid was developed in Illinois and Iowa and was mostly Southern Dent. Lancaster was developed in Pennsylvania, in relative isolation from Reid and the rest of the Corn Belt cultivars, and had a higher percentage of Northern Flint in its background. This geographic and phylogenetic history was the basis for the excellent combining ability between Reid and Lancaster inbreds.

To distill the story to its essence: The major heterotic pattern in Corn Belt Dent is based on geographic /phylogenetic distance of the source germplasm and therefore the Reid – Lancaster pattern was waiting to be discovered. The whole story made perfect sense and, for me at least, became the orthodox or canonical (to use Stephen J. Gould's term, Gould, 2002) story of the biological basis of heterotic groups. From lectures and writings of other plant breeders (e.g. Havey, 1998; Melchinger and Gumber, 1998; Cheres, et al., 2000), I believe this has become the canonical story regarding CBD heterotic groups for many breeders.

The late Stephen J. Gould, evolutionist and essayist, often wrote about canonical stories in biology (Gould, 2002). He believed that canonical stories, like folk tales, teach important lessons in a simplified, easily remembered way. He also believed that canonical stories could get in the way of our understanding of complex biological systems. Gould wrote a number of essays on canonical stories, explaining what the intended message was and explaining what we as scientists were missing due to the oversimplification of complex systems. Put simply, if a story is too good to be true it probably isn't. And so it is with the Reid by Lancaster heterotic groups.

The main message of the Reid - Lancaster story for novice plant breeders is clear, simple, and important. Genetic diversity is needed for high levels of heterosis. However, for many, the canonical story of CBD heterotic patterns may be misleading. For example, if we accept that Reid by Lancaster heterosis is due to a historical contingency, the geographic isolation of these two varieties, and that all important hybrids are based on this pattern, we would draw certain logical conclusions. We might conclude that when beginning a hybrid breeding program one should search for maximum diversity, create groups by dividing the germplasm along the lines of maximum diversity, and develop hybrids by making crosses between inbreds derived from different groups. The validity of such a conclusion, however, depends on the factual basis of the canonical story. Specifically, are most important CBD hybrids based on the famous Reid – Lancaster pattern? And are high levels of heterosis due to the geographically diverse origins of Reid and Lancaster? Our intent is to look more deeply at the historical and biological basis of the concept of CBD heterotic groups and see if the canonical story leads to a misunderstanding of the process.

In this paper we will address four questions: 1. What issues confronted early hybrid corn breeders? 2. When did the concept of heterotic groups develop in the Corn Belt? 3. What was the actual role of Lancaster? (Was geographical isolation of Lancaster required for the success of hybrid corn?) 4. How did CBD heterotic groups develop?

Methods

We reviewed corn breeding literature focusing primarily on the U.S. There are many excellent corn breeding reviews and books and these were examined, but, whenever possible we went to the primary literature. We looked for articles covering heterosis or combining ability in corn in the indices of all volumes of Crop Science and in the Agronomy Journal between 1920 and 1980. We reviewed the table of contents of all the Proceedings of the American Seed Trade Association Corn and Sorghum Research Conferences and the Proceedings of the Illinois Corn Breeders School. We reviewed the minutes from all the meetings of the North Central Region Corn Improvement Conferences up until 1985. Potentially rich sources of primary literature we did not review are the numerous experiment station bulletins, reports, and circulars.

A Brief History of Hybrid Corn

Hybrid corn was such a major technological and economic event that a number of excellent histories have been written (Crabb, 1942; Wallace and Brown, 1956; Hayes, 1963; Hallauer et al, 1988; Hallauer, 1999).

E.M. East (1908), G.H. Shull (1908) and others experimented on inbreeding corn in the early 1900s. In the first decade of the twentieth century, Shull (1908, 1909, 1952) made three key observations; 1) individual plants in a normal corn OPV were hybrids, 2) by inbreeding, hybrids could be reduced to true breeding strains (inbreds), and 3) uniform hybrids could be produced by crossing two inbreds. East was in the audience when Shull first publicly discussed his results and recognized the importance of Shull's discovery and the relevance of his own work to corn improvement (Shull, 1952; Singleton, 1963).

Shull moved on to other genetic research but East and his students continued research on inbreeding and crossbreeding corn (Hayes, 1963). East's students became the leading corn breeders and geneticists of the next generation, and were instrumental in the development of hybrid corn (Peterson and Bianchi, 1999).

Despite the scientific interest surrounding Shull's discovery, hybrid corn did not appear economically viable (Baker, 1984). This was because the inbreds developed directly from OPVs were very weak and could not produce quantities of seed at prices farmers would pay. D.F. Jones overcame this problem with the invention of the double cross hybrid (Jones, 1918). A double cross is created by making two single cross hybrids (A X B) and (C X 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. Double cross hybrids were first sold in the Midwest in the 1930s and were rapidly accepted by Midwestern farmers. By 1943 nearly all of Iowa corn acreage was planted to hybrid corn and by 1960 virtually all US corn was hybrid (Hallauer and Miranda, 1981; Sprague, 1983). While hybrids yielded 10 to 20% more than open-pollinated cultivars, other traits of the new hybrids also played a role in the rapid acceptance of hybrids. Hybrids came on the scene as hand harvesting was being replaced by mechanical harvesting and hybrid traits such as increased uniformity and decreased lodging were highly valued.

The first inbreds were derived by self-pollinating plants from the numerous OPVs. Later generations of inbreds were developed by intermating existing inbreds and then selfing in a pedigree breeding program. As a result of selection and recombination, later cycle inbreds were more vigorous and higher yielding. Some of the improved inbreds could produce economic levels of hybrid seed directly. In the 1960s single cross hybrids began to replace double crosses and by the mid-1980s nearly all new hybrids were single crosses (Hallauer et al., 1988).

Issues confronting early hybrid corn breeders

The number one issue confronting early hybrid corn breeders was the poor agronomic quality of the first generation of inbreds derived directly from OPVs. In 1984 Raymond Baker (1984) wrote

> "*Just keeping those early inbreds from open-pollinated corn alive was an art… Most practical breeders predicted that hybrid corn would never succeed because of these weak rooted first cycle inbreds*."

George Sprague (1984) recalled that in the Iowa breeding program, Lancaster made good inbreds (combining ability) but were all so weak rooted that only two were named and released, L289 and L317.

The invention of the double cross (Jones, 1918) allowed these weak inbreds to be used commercially but breeders wanted to develop improved inbreds.

Early hybrid corn breeders were developing theory as they developed new inbreds and hybrids. The relationship between genetic divergence and combining ability was initially unclear and required 20 to 30 years of research before the relationship was firmly established. Since this relationship was unclear and breeders needed to improve inbred performance they made breeding crosses among elite inbreds. The crosses were designed so that weaknesses in one inbred were compensated by strengths in the other. Less attention was given to maintaining diversity.

Richey (1927) suggested the breeding scheme called convergent improvement to test the dominance theory of heterosis. Convergent improvement is a double backcross program in which the F_1 (A x B) is backcrossed to each parent A and B. Richey (1927) hypothesized that if heterosis was due to dominance it should be possible to improve the performance of the inbreds by accumulating favorable dominant alleles in A' and B' without altering the performance of the hybrid. Experiments by Richey and Sprague

(1931) and Hayes and students at Minnesota (Murphy, 1942) supported this approach but the method was not widely used by corn breeders.

Convergent improvement is, in fact, a program to breed for decreased diversity between the parents of the hybrid. Furthermore, since its purpose is to improve inbred performance without altering hybrid performance, if effective, it will result in decreased heterosis. Sprague (1955) and Sprague and Eberhart (1977) devoted considerable space to convergent improvement in corn breeding chapters in the first and second editions of *Corn and Corn Improvement*. In the third edition, Hallauer et al. (1988) briefly mention convergent improvement but say that it is not widely used. While never much used, the persistence of convergent improvement in the literature indicates that the imperative of inbred improvement outweighed the need for maintaining or increasing diversity.

In 1950 Richey (1950) wrote,

> *"This would lead to the expectation that crosses between inbreds from different varieties would tend to be more productive than crosses between inbreds of the same variety. This expectation has been justified by the general experience of corn breeders"*.

A few years later Griffing and Lindstrom (1954) wrote,

> *"Corn breeders have frequently suggested that the degree of heterosis is to some extent proportional to the genetic divergence of the parent inbreds. If this hypothesis is correct…"*

These quotes from leading corn breeders and geneticists indicate that the relationship between diversity and combining ability was still not settled in the 1950s. The work of Lonnquist, Moll, and collaborators (Lonnquist and Gardner, 1961; Moll et al. 1962; Paterniani and Lonnquist, 1963) finally settled the issue more than 40 years after hybrid corn breeding began.

While corn breeders in the 1940s and 1950s began to establish the relationship between diversity and its role in combining ability, the need to develop improved inbreds was an overriding concern. Thus, many second and third cycle inbreds were derived from crosses between parents from what we now consider opposite heterotic groups. This was especially true with Lancaster germplasm, which had relatively poor root and stalk quality. As a result most second cycle Lancaster inbreds were, by pedigree, 50% or less Lancaster (Gerdes and Tracy, 1993) (Table 1.)

As the number of publicly developed inbreds proliferated, corn breeders were confronted with another problem; how to organize the inbreds to make breeding programs more efficient? In 1947 G.S. Stringfield, corn breeder at the Ohio Agricultural Experiment Station, raised this issue at the annual meeting of corn breeders from the North Central Region, the North Central Regional Corn Improvement Conference. Following is a direct quote from the minutes of the 1947 meeting.

> *"G.H. Stringfield discussed the advisability of grouping lines for breeding purposes. He urged that crosses for the improvement of lines then should be made only among lines of the same group The object would be to maintain genetic diversity and avoid relationships among lines that*

later are used in the production of hybrids." (Anon., 1947).

A committee was formed to study the situation and suggest such a program of operation for the Corn Belt. The conference did not meet in 1948 but at the 1949 meeting the "Committee on Grouping of Inbred Lines for Breeding Purposes" presented the following report (Anon., 1949).

> *"The committee recommends that the inbred lines of the North Central Corn Improvement Conference be divided into two groups, which are to be kept distinct in breeding advance cycle lines. This means that no crosses for breeding purposes are to be made except between lines belonging to the same group.*
>
> *Each group should contain inbreds representing widely diverse maturities and desirable plant characters. As an arbitrary division, the committee recommends that the lines having odd entry numbers in the 1948 uniform tests of inbreds be tentatively assigned to Group A and that those having even entry numbers be tentatively assigned to Group B. In cases of known relationship between inbreds, the originating station shall be responsible for shifting lines to provide for maximum genetic diversity between groups.*
>
> *It is recommended that each station submit a revised list to the committee in order that a permanent grouping may be presented at the next meeting of the conference."*

This report was moved and passed by the conference and became the policy of the committee through the late 1980s.

Given a 2004 perspective it appears that this plan was the beginning of what we now call heterotic groups. But notice the way in which the lines were assigned, odd numbers in group A and even in group B. The next sentence did address the issue of relationship among inbreds and maximum genetic diversity between groups. But a review of the lists shows that the breeders' understanding of relationship did not reflect the canonical story (Reid – Lancaster). The first list released in 1950 shows that most states followed the odd – even scheme and closely related lines ended up in both groups, e.g. inbreds I205 (Iodent), L317 (Lancaster), and Os420 (Osterland Reid) were in group A while, I159 (Iodent), L289 (Lancaster), and Os426 (Osterland Reid) were in group B. B10 one of the first inbreds developed from Iowa Stiff Stalk Synthetic (BSSS) was assigned to group B (Anon., 1950).

BSSS, a source of many important inbreds, is a 16 line synthetic developed by George Sprague in the 1930s. Seventy five percent of BSSS background traces back to improved strains of Reid Yellow Dent (RYD) (Troyer, 2000b). Therefore BSSS inbreds are usually classified as a subgroup of the Reid heterotic group (Troyer, 2000a).

The second list was published in 1953 (Anon., 1953). New inbreds were added and some inbreds were moved to the opposite group to better reflect their origin. But, there were still cases of inbreds from the same OPV assigned to both groups. Most of the important Reid and Lancaster inbreds were assigned to group A, clearly indicating that in 1953 the leading corn breeders did not recognize the Reid – Lancaster heterotic pattern of the canonical story. All of the BSSS inbreds were in group B. This arrangement persisted through the 1980s when the committee for grouping inbred lines was discontinued.

In 1971, there was some discussion regarding the usefulness of the groups. In that discussion Dr. Steve Eberhart was quoted as follows

> "*heterosis depends on differences in gene frequencies and dominance effects so that on the average, greater heterosis is observed between divergent groups. Since the A and B groups were originally established on the basis of heterosis between Midland and Reid types, the grouping has and could continue to serve its purpose…*"

(Anon., 1971). While there is now no dispute with the first sentence, a thorough review of the committee minutes from 1947 to 1971 found no evidence that the groups were originally formed around a Midland – Reid heterotic pattern. Indeed the early lists had few, if any, Midland lines (Anon., 1950, 1953).

History of the Concept of Heterotic Patterns

Today, the concept of heterotic patterns seems fundamental to our ideas on breeding hybrid crops. But the concept and terminology were expressed in modern terms 40-50 years after the beginning of hybrid corn breeding. George Sprague (1984) wrote

> "*In retrospect it appears that the concept of heterotic patterns was slow in developing.*"

Since CBD heterotic patterns developed empirically (Hallauer and Miranda, 1981; Hallauer, 1999; Troyer, 2000a), yield testing of many hybrids had to be done before any patterns could become obvious (Hallauer, 1999; Hallauer et al., 1988). Ideas and observations underlying the concept of heterotic patterns (combining ability, grouping of inbreds, relationship between diversity and heterosis, and recognition of the importance of specific OPVs) needed to develop prior to the development of our current concepts. Published observations on the importance of inbreds derived from Reid, Krug, and Lancaster began in the 1940s (Anderson, 1944). Krug is an improved strain of Reid (Gracen, 1986).

Public and private breeders began grouping inbreds in the 1950s (Smith et al., 1999). Dr. D. Duvick, retired research director of Pioneer Hi-bred, recalled that groups were initially created based on whether the inbred was an acceptable seed parent or pollen parent. B37, a public inbred used by Pioneer in the 1950s, was a good seed parent but was not a good pollen producer. It became part of the "female" group (D. Duvick, pers. comm.). B37 was derived from BSSS and other BSSS related inbreds were also eventually placed in the female pool. Inbreds that combined well with BSSS were placed in the male pool. In publications by Pioneer researchers, the Pioneer female pool is also called stiff stalk (SS) and the male pool is designated non-stiff stalk (non-SS) (Smith et al., 2000, Romero-Severson et al., 2001, Casa et al., 2002; Duvick et al., 2004).

The first mention of the term heterotic pattern (or heterotic group) that we could find in the literature was in 1972 by B. Tsotsis (1972), then director of corn breeding with Dekalb Agresearch Inc. Tsotsis (1972) discussed the Reid – Lancaster heterotic pattern and research designed to identify new heterotic patterns. Tsotsis (1972) attributed the research to unpublished work of C.W. Crum of Dekalb Agresearch in 1970. Thus, it is clear that our current concept of heterotic patterns was familiar to some corn breeders at least by the late 1960s. The work by the Dekalb group, Crum, Kaufman, and Tsotsis focused on developing new heterotic patterns (Tsotsis, 1972; Crum, 1973; Kaufman, et al., 1982). Their methodology and experimental design were similar to the earlier work of Lonnquist and Moll and collaborators (Lonnquist and Gardner, 1961; Moll et al., 1962; Paterniani and Lonnquist, 1963). But these workers did not discuss their work in terms of identifying heterotic patterns or groups.

Discussions on heterotic patterns are then found in corn breeding literature, e.g. Proceedings of the ASTA Corn and Sorghum Research Conference, Proceedings of the Illinois Corn Breeders School, minutes of the North Central Regional Corn Improvement Conference, occasionally in the 1970s and early 1980s (Crum, 1973; Beil, 1975; Kannenberg, 1976; Kaufman et al., 1982). Hallauer and Miranda (1981) discuss heterotic patterns in *Quantitative Genetics in Maize Breeding*. Hallauer et al. (1988) devote five pages to the topic of heterotic patterns in the corn breeding chapter of the third edition of Corn and Corn Improvement (Sprague and Dudley, 1988).

Perhaps more revealing is where the terminology did not appear. No mention of heterotic groups or patterns are found in the books *The Hybrid Corn Makers* (Crabb, 1942), *Corn and Its Early Fathers* (Wallace and Brown, 1956), *A Professors Story of Hybrid Corn* (Hayes, 1963), Corn (Manglesdorf, 1974) or numerous important chapters about corn breeding (Anderson and Brown 1952; Jenkins, 1978; Russell and Hallauer, 1980; Zuber and Darrah, 1987; Sprague, 1983). Some of these books and book chapters did mention Reid – Lancaster hybrids and/or groups or families of inbreds but they did not use the terms heterotic groups or patterns. George Sprague, one of the leading corn breeders and corn breeding theoreticians of the 20th century, edited all three editions of *Corn and Corn Improvement* (Sprague, 1955, 1977; Sprague and Dudley, 1988). He also wrote the corn breeding chapters in the first and second editions (Sprague, 1955; Sprague and Eberhart, 1977). In the first edition Sprague (1955) does not mention heterotic groups or patterns nor does he mention Reid or Lancaster. In the second edition, Sprague and Eberhart (1977) mention the importance of Reid, Lancaster, and Krug germplasm. They do not mention heterotic groups or patterns. In sharp contrast, just seven years later in a lecture to the Illinois Corn Breeders School, Sprague (1984) said,

> "*The single most important element of a breeding program is the recognition and utilization of heterotic patterns, this recognition simplifies and increases the efficiency of all subsequent operations*."

Clearly the concept of heterotic groups grew from a minor point to a major concept during the 1970s and early 1980s.

The terms "heterotic group", "heterotic groups", " heterotic pattern", and heterotic patterns" were seldom used in literature included in databases such as Agricola and CAB until the late 1980s

(Table 2, Fig. 1). Searching different databases resulted in different numbers of citations and different year of first use. But the overall pattern is quite consistent (Table 2) The CAB database resulted in more citations than Agricola and the largest number of citations, 122, resulted from searching the term “heterotic groups”. In contrast searching the CAB database for “combining ability” resulted in 9,039 citations going back to 1972, the earliest year of the CAB database. The earliest citation using any of the terms related to heterotic groups was a 1978 abstract by Mishra and Geadelmann (1978). The earliest refereed publications to use “heterotic groups” were in 1986 with one paper on wheat (Murphy et al., 1986) and another on corn (Smith, 1986).

The terms dealing with heterotic groups or patterns were seldom used prior to the late 1980s and then use increased dramatically (Fig. 1). Many of the papers referring to heterotic patterns from 1987 through 2003 dealt with the use of DNA-based markers for sorting germplasm into heterotic groups. The first papers describing RFLPs for use in maize breeding and genetics appeared in the mid 1980s (Helentjaris et al., 1985; Evola et al., 1986). In 1987, Walton and Helentjaris (1987) presented a paper on the use of RFLP technology in maize breeding at the ASTA corn and sorghum research conference. The first use they listed was “organization of germplasm” (Walton and Helentjaris, 1987).

In summary, our current concept of heterotic patterns crystallized in the late 1960s and early 1970s and became widely recognized and accepted in the 1970s and early 1980s. It is unclear why the concept of heterotic groups developed when it did. Many of the ideas underlying the concept were developed earlier and the importance of Reid and Lancaster was recognized much earlier. It may be that the change to single cross hybrids in the 1960s and the importance of Reid (Wf9, B14, B37) and Lancaster inbreds (C103, C123, Oh43, Mo17) in these early single crosses made the concept of heterotic patterns quite clear and useful.

What was the actual role of Lancaster?

A key feature of the canonical story of CBD heterotic patterns is that Lancaster germplasm was uniquely important and by implication, geographical isolation of Lancaster was required for the success of hybrid corn in the Corn Belt. The current and historical importance of Reid inbreds especially in the form of BSSS inbreds is very clear, but what was the actual role of Lancaster?

The excellent combining ability of three Lancaster inbreds, L289, L317, and LDG was noted by Edgar Anderson (1944) in 1944. Anderson was not a corn breeder and he received this information from Raymond Baker, manager of the breeding department of Pioneer Hi-Bred Corn Company. Anderson reported on the inbreds in six of the most widely grown hybrids. All the hybrids were double crosses. He noted that 18 different inbreds were used in these crosses, 12 of which were from Reid Yellow Dent, 3 from Krug, and 3 from Lancaster (Table 3). Anderson (1944) suggested that contributions of Reid and Krug were unsurprising due to the importance and wide use of these OPVs in the Corn Belt. He was very surprised that Lancaster, an obscure OPV from Pennsylvania, had such a significant impact. He wondered

> "*If Lancaster Surecropper is really an effective source of good inbreds is there anything in its history to suggest why this might be so?*"

Of the six double cross hybrids studied by Anderson (1944) four had one Lancaster inbred (Table 3). The remaining two had no Lancaster contribution. One was all Reid and the other was 50% Reid and 50% Krug (Reid).

Other authors noted the importance of Lancaster inbreds in CBD hybrids (Crabb, 1942; Anderson and Brown 1952, Wallace and Brown, 1956). Interestingly Crabb (1942) in The Hybrid Corn Makers briefly mentions Lancaster inbreds L289 and L317, but does not include a discussion of Lancaster or its developers, while there were lengthy discussions on Reid and Krug. The 1992 reprinting of his book has significantly more information on Lancaster and its developer Isaac Hershey (Crabb, 1992). Clearly awareness of Lancaster increased over time.

The initial observations of the importance of Lancaster inbreds were based on their contributions to important hybrids of the 1930s such as US13 - (Wf9 x 38-11) (HY x L317) and Iowa 939 - (I205 X L289) (Os420 X Os426), two of the most popular hybrids in history. George Sprague (1964, 1984) discussed the importance of Lancaster inbreds and mentioned that their uniqueness was very apparent in the Iowa program. Later Oh43 and Mo17 (both 50% Lancaster) and their derivatives became important in the 1960s and 1970s. B73 X Mo17, the most important public single cross of the 1970s and 1980s, probably played an important role in popularizing the canonical story. Raymond Baker (1984) pointed out that

> "*typically modern hybrids have one inbred parent derived from Iowa Stiff Stalk Synthetic. The other side of the cross usually has some Lancaster in its origin. Usually, the non Stiff Stalk parent is only half Lancaster with Reid or some northern variety like Minnesota 13 as the other half.*"

Zuber and Darrah (1981) reported that in 1979 39% of the U.S. germplasm was related to Lancaster and 42% to Reid. Zuber and Darrah grouped Oh43 and Mo17 as 100% Lancaster (Darrah, pers. comm.). Since both these inbreds and all their derivatives are no more than 50% Lancaster by pedigree, 39% Lancaster is an overestimate and 42% is an underestimate for Reid. Five years later, the Lancaster contribution had dropped to 12% with 44% Reid and 24% Iodent (Darrah and Zuber, 1986).

It is clear that public sector breeders recognized the importance of Lancaster in CBD hybrids, but much of the written record on Lancaster's importance was retrospective, after Mo17 and Oh43 had significant impacts. A closer look at the both the historical and current impact of Lancaster tells a different story.

Of the six hybrids discussed by Anderson (1944) four had one Lancaster line (Table 3). Of the remaining two hybrids, one had four Reid inbreds and the other two Reid and two Krug. Since Krug is an improved strain of Reid, on a percentage basis Reid constituted 83.3% of these six hybrids and Lancaster 16.7%.

Russell (1974) studied the contribution of breeding to increased corn yields by comparing hybrids from different decades in replicated yield trials. He chose four hybrids from each decade. The hybrids were chosen because they were among the most popular and widely grown in central Iowa. The contribution of Reid and Lancaster was calculated as the % contribution by pedigree totaled over the four hybrids from each decade (Fig. 2). These numbers were calculated based on the estimated pedigree contribution, e.g. Mo17 is 50% Lancaster and 50% Krug (Reid). All inbreds derived from BSSS were grouped with Reid. The four most popular hybrids all had similar pedigrees in the 1930s. Each had three Reid inbreds and one Lancaster (Fig. 2). Since Anderson (1944) wrote on sources of important germplasm in 1944 these and similar hybrids would have formed the data set he used. What would Anderson have written if he had based his conclusions on hybrids of the 1940s or 1950s rather than the 1930s? In the 1940s Reid accounted for 82.5% of the hybrids, Lancaster only 6.25% (Fig. 2). In the 1950s there was no Lancaster germplasm in the four hybrids. In the 1960's Lancaster's share increased to 4.69%. With the advent of the single cross, the Lancaster contribution increased to 25%, the historical high in the 1970s. Clearly Lancaster was not required for successful commercial hybrids. Recently published papers documenting the contribution of germplasm to Pioneer Hi-Bred's commercial hybrids support this conclusion (Smith et al., 1999; 2004; Romero-Severson et al.; 2001; Casa et al., 2002; Duvick et al., 2004). In Pioneer's program, Lancaster contribution peaked in the 1940s (16.9%) and has since declined to historic lows in the 1990s (2.9%) (Smith et al., 1999). Duvick et al. (2004) put the current Lancaster contribution to a series of successful hybrids for the west-central Corn Belt at 3.45%. Smith et al. (2004) estimated the Lancaster contribution at 4.9% and that of Lindstrom Long Ear at 2.9%. Troyer (2004) has suggested that Lindstrom Long Ear was derived from Lancaster. Is this is so it would raise the contribution of Lancaster to 8% in current Pioneer germplasm. While significant, clearly Lancaster is not a major component of Pioneer's successful breeding program.

Smith et al. (1999) suggest that Lancaster was more important in the public sector than it was for Pioneer. However, the proportion of Lancaster in public sector Lancaster inbreds has decreased with each cycle of breeding (Table 1) (Gerdes and Tracy, 1993).
First cycle inbreds such as L317 and C103 were 100% Lancaster. However, with each cycle of breeding the proportion of Lancaster was reduced by 50%. While foundation seed companies still group families with names such as Mo17 or C103 (Anon., 1995), it is clear based on the morphology of these newer inbreds that they have substantial amounts of non-Lancaster germplasm. Williams and Hallauer (2000) wrote that the primary guide used to classify an inbred as Lancaster is that the inbred exhibit good combining ability with lines from BSSS.

What was the true role of Lancaster? With a few exceptions successful hybrids were never more than 25% Lancaster. Many successful modern hybrids have no Lancaster by pedigree, and for those that do the percentage of Lancaster is probably less than 12.5% (Gerdes and Tracy, 1993; Troyer, 2000a; Romero-Severson et al. 2001, Casa et al 2002). Troyer (1999) indicated that Lancaster contributed approximately 4%

by pedigree to commercial germplasm. The declining influence of Lancaster can be seen in the terminology used in the literature. The heterotic pattern was first described as Reid – Lancaster (Tsotsis, 1972; Hallauer and Miranda 1981). Later as the contributions of BSSS became clear, the pattern was usually called Stiff Stalk – Lancaster (Geadelmann, 1984; Dudley, 1984). Today knowledgeable writers discuss Stiff Stalk – Non-Stiff Stalk (Casa et al., 2002; Duvick, 2004).

If the role of Lancaster is overstated, what is the origin of the canonical story? Anderson's paper in 1944 hinted at a unique place of Lancaster in the success of hybrid corn. But, the Anderson and Brown (1952) paper in the book *Heterosis* (Gowan, 1952) explicitly stated

> "*…sources of good combining inbreds are open-pollinated varieties with a stronger infusion of Northern Flint than was general in the Corn Belt. This is particularly true of Lancaster Surecrop…*"

This is the essence of the canonical story and probably its original written source. The 1950 Heterosis Symposium was influential and the resulting book, *Heterosis* (Gowan, 1952), was widely read and cited. It is clear from later writings that Dr. William Brown, later president of Pioneer Hi-Bred, was convinced of the importance of the Northern Flint germplasm in determining Lancaster's combing ability (Brown, 1953; 1967; Weatherspoon, 1973).

How did CBD heterotic patterns develop?

Corn Belt Dent heterotic patterns developed empirically by trial and error, based on crosses among inbreds initially derived from the available OPVs (Hallauer et al., 1988; Hallauer, 1999; Troyer, 2000a). Hallauer (1999) wrote

> "*Heterotic groups do not evolve naturally except for being genetically dissimilar for allele frequencies*."

When hybrid breeding began, breeders had a number of OPVs available to them, but the choice of patterns was not systematic (Hallauer et al, 1988). Later, breeders including Tsotsis (1972), Crum (1973), and Kaufman (1982) attempted to identify new CBD heterotic patterns by systematic crossing. Once heterotic groups have been established and improved by breeding, however, it is difficult to develop competitive new patterns (Hallauer et al., 1988; Melchinger, 1999).

The number and choice of heterotic groups are arbitrary decisions. Some breeders prefer a large number of specific groups (Troyer, 2000a), while others prefer to arrange their program based on two large, diverse groups (Hallauer et al, 1988, Hallauer, 1999). When two main groups are used there are usually subgroups within the main groups (Hallauer et al, 1988). SSS - Lancaster is the best known CBD heterotic pattern because it fits well with grain requirements for the main type of corn (No. 2 yellow), is adapted to the central Corn Belt, and was developed by the public sector. White corn was more important in Tennessee and Kentucky and the consumer would not tolerate yellow kernels in the corn. Thus a number of the successful early double cross hybrids consisted of four inbreds from the same white OPV (Hayes, 1963; Jenkins, 1978). Troyer (2000a) lists a number of alternate heterotic groups that fit the northern Corn Belt better than

SSS - Lancaster. If the main part of the Corn Belt was 200 miles north, the most famous heterotic group may have been Reid - Minnesota 13. It is now apparent that the most important heterotic pattern for Pioneer Hi-Bred in the central Corn Belt is not SS - Lancaster but instead SS - non-SS. Pioneer non-SS has a large contribution from Iodent and Minnesota 13 with a smaller contribution from Lancaster (Romero-Severson et al. 2001, Casa et al 2002).

All inbreds within CBD heterotic groups are not necessarily related (Geadelmann, 1984; Casa et al., 2002; Duvick et al., 2004). What the inbreds have in common is high combining ability with inbreds from the opposite heterotic group (Hallauer et al., 1988; Williams and Hallauer, 2000). When an inbred unrelated to either group in a heterotic pattern combines equally well with inbreds from the two groups, the breeder must choose the group into which the inbred is incorporated. Geadelmann (1984) wrote that when such a situation occurred he essentially "flipped a coin" in assigning the germplasm to a group. Of the two main CBD groups, SS and non-SS, it appears that the SS group is more homogeneous than the non-SS (Casa et al., 2002; Liu et al., 2004).

Heterotic groups are not constant, nor absolute (Hallauer et al, 1988; Gerdes and Tracy, 1993; Smith et al., 1999). The genetic composition changes over time. The public Lancaster group has become less Lancaster and more Reid with each cycle of breeding (Gerdes and Tracy, 1993).

Pioneer Hi-Bred has documented the change in its germplasm (Smith et al., 1999, 2004). This information makes an excellent case study on heterotic groups and especially the aspect of the canonical story that phylogenetic distance based on geography or some other historical contingency is needed for the creation of successful heterotic groups.

Pioneer began grouping inbreds in the 1950s, roughly the same time that the public sector began to do so (Anon., 1950; Smith et al., 1999; Duvick et al., 2004; Duvick, pers. comm.). The initial criteria for grouping included whether the inbreds made good seed or pollen parents (Duvick, pers. comm.). B37 a good seed producer and a poor pollen shedder was placed in the female pool, which evolved into the SS group. Inbreds that were good pollen shedders, unrelated to SS, and combined well with SS were placed in the non-SS group. The groups were formalized between 1960 and 1989 (Duvick et al., 2004). Pioneer was never as dependent on Lancaster inbreds as was the public sector and some other companies (Smith et al., 1999). Pioneer's highest use of Lancaster was in the 1940s with about 15% and the 1970s (8.6%). In the 1990s, Lancaster contributed approximately 3% to Pioneer commercial hybrids (Smith et al., 1999).

If Lancaster is not the main constituent of the non-SS group, what is? A major constituent of the Pioneer non-SS pool is "Pioneer Iodent" (Romero-Severson et al., 2001, Casa et al., 2002). Iodent OPV was an early-maturing strain of Reid selected at Iowa State College (Troyer, 1999). However, Pioneer Iodent inbreds are not pure Iodent (Hallauer and Miranda, 1981; Troyer, 1999; Romero-Severson et al., 2001). While the highest contribution is Iodent, they have a diversity of germplasm sources including other Reid strains and northern and southern germplasm. The most consistent component following Iodent is Minnesota 13. Of the germplasm backgrounds of five Iodent inbreds revealed in Romero-Severson et al. (2001) only one has any Lancaster. A number of these inbreds do have Lindstrom Long Ear in their pedigrees and if Lindstrom Long Ear was derived from Lancaster, as Troyer (2004) suspects, most of these inbreds would have some Lancaster. When the germplasm sources are totaled most of the five inbreds are 50% or more Reid (Iodent plus Reid sources) (Romero-Severson et al. 2001). Thus both groups in the Pioneer pattern are more than 50% Reid. **This does not fit the canonical story. The Pioneer heterotic groups are not derived from material that was geographically or phylogenetically distant. Substantial portions of Pioneer's SS and non-SS are derived from the same cultivar.** The predominance of Reid in Pioneer's current heterotic groups was summarized by Smith et al. (2004) as follows

> *"…a performance potential that was previously latent in RYD has been realized as evidenced by the combining ability of lines developed from BSSS (largely Reid) when crossed to lines that are predominantly Iodent, a strain of Reid"*

Duvick et al. (2004) examined SSR polymorphisms among the inbred parents of the hybrids in the Pioneer era studies. In the era studies widely grown hybrids from different decades are compared to determine the changes that have occurred over time and the proportion of change that is due to genetics and breeding (Duvick et al., 2004). Duvick et al. (2004) found that the inbreds from the pre-heterotic group era formed one large cluster with no clear groupings (Fig. 3). On the other hand the modern SS and non-SS inbreds form discrete groups divergent from one another and the pre-heterotic group cluster. Duvick et al. (2004) wrote

> "*The SSR polymorphism data indicate a clear divergence between the allele profiles of the inbreds created by pedigree breeding in the SS and the non-SS heterotic groups.*"

The divergent groups were created by breeders. They did not exist in the original germplasm.

Summary

Heterotic patterns are useful tools for increasing the efficiency of breeding programs, but breeders should be wary of adhering to the canonical story too rigidly. Corn breeding abounds with examples of successful breeders who developed very important inbreds from crosses between parents from the two heterotic groups. Indeed this may be a crucial factor in inbred development. If there is a group of elite inbreds with many excellent characteristics but deficient in some character such as root quality, the best source of improved roots may be inbreds from the opposite group. Because there are usually numerous subgroups within groups it is possible to make intergroup crosses and still develop excellent inbreds that have excellent combining ability.

The first breeders of hybrid corn were confronted by a number of problems, perhaps, the most important of which was that first cycle inbreds were extremely weak and difficult to maintain. These breeders needed to develop improved inbreds and they did it by crossing the best inbreds available with relatively little regard for relationships among the inbreds. An excellent example is Mo17, which was derived from a cross between a Lancaster inbred and a Krug (Reid) inbred.

A second problem confronted by early breeders was one of organization; how to organize the breeding program with the flood of inbreds being developed by public breeders. Breeders in the 1940s chose to do this by splitting the inbreds into two groups and creating the groups in an apparently arbitrary way with little attention to phylogeny. While this may seem surprising, there is theoretical, experimental, and empirical support for this approach. Cress (1967), based on the results of computer simulations, 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). Butruille et al. (2004) did exactly this in an experimental population. After six cycles of recurrent selection, they detected a significant increase in the yield of the population cross. Allele frequencies diverged, but it was not possible to determine if the changes were due to drift or selection (Butruille et al., 2004). The empirical date from the Pioneer breeding program as shown in the Era experiments also lends support to the actions of the breeders in the 1950s. Pioneer breeders started with inbreds derived from CBD OPVs. Using SSRs it was not possible to determine any population structure among these progenitor lines (Duvick et al. 2004). After 60 years of selection, distinct heterotic groups were detected using molecular markers (Duvick et al., 2004). In a separate study on the population structure of CBD OPVs, Labate et al. (2003) found no evidence of two broad groupings of Reid and Lancaster.

Conclusion

Parts of the canonical story are incorrect; CBD heterotic patterns were created by breeders, and are not the result of historical or geographical contingencies. The canonical story originated from an article by Anderson and Brown (1952) based on successful hybrids of the 1930s. The concept of heterotic patterns developed in the 1960s and 1970s. Academic interest in heterotic patterns increased in the late 1980s. Academic interest was stimulated by the availability of DNA based markers and attempts at using markers to identify heterotic patterns. Such examinations have shown that it would not have been possible to identify heterotic groups for CBD OPVs and first cycle inbreds using molecular markers, had they been available in the early years of hybrid corn breeding (Labate et al., 2003; Duvick et al., 2004). If breeders had been able to identify Lancaster in the 1930s and tried to keep the Lancaster group pure, breeding progress would have been greatly impeded (poor agronomics of Lancaster).

CBD heterotic patterns were created by breeders through trial and error from a single race of corn. Using heterotic groups as a tool in a hybrid breeding program results in divergent heterotic groups.

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Table 1. Background and percent Lancaster contribution to background of 27 inbreds classified in the Lancaster heterotic group ranked in order of decade of release (Gerdes and Tracy, 1993).

Inbred	Background	% Lancaster (by pedigree)	Decade of release
L289	Lancaster OP	100	1920
L317	Lancaster OP	100	1920
C103	Lancaster OP	100	1940
Oh43	Oh40B x W8	50	1940
Mo17	C.I. 187-2 x C103	50	1960
A619	(A171 x Oh43)Oh43	37.5	1960
Pa375	CH22 x C103	50	1970
H95	Oh43 x C.I.90A	25	1970
Va26	Oh43 xK155	25	1970
Va35	(C103 x T8)T8	25	1970
B70	M14 x C103	50	1970
Oh570	Oh07 x C103	50	1980
Oh572	Oh07 x C104	50	1980
A682	[(AS-D x Mo17)M017(2)]	40.6	1980
A683	[(AS-D x Mo17)M017(2)]	40.6	1980
H108	(Mo17 x H99)Mo17	40.6	1980
H109	(Mo17 x H99)Mo17	40.6	1980
N197	(Mo17 x Early Krug line)Mo17	37.5	1980
N198	(Mo17 x Early Krug line)Mo17	37.5	1980
Pa869	75F-5 x Pa83	25	1980
Pa870	75F-5 x Oh43	25	1980
T167	Mo17 x C.I.66	25	1980
H107	(H99 x H98)H99	15.6	1980
CM555	(Mo17 x MAG)MAG	12.5	1980
NC258	Complex pedigree	12.5	1980
NC260	(Mo44 x Mo17)Mo44	3.1	1980
B93	B70 x H99)H99	21.9	1990

Table 2. Number of citations and the year first cited for the key words; heterotic group, heterotic groups, heterotic pattern, heterotic patterns, heterotic pool, heterotic pools, and combining ability. Inclusive years were 1967-2002 for Agricola and 1973 – 2002 for CAB.

	Database			
	Agricola		CAB	
Key words	Number of citations	Year first cited	Number of citations	Year first cited
Heterotic Group	17	1987	43	1986
Heterotic Groups	42	1986	122	1978
Heterotic Pattern	17	1990	53	1980
Heterotic Pattern	26	1988	68	1984
Heterotic Pool	1	1998	2	1998
Heterotic Pools	0	-	7	1987
Combining Ability	2062	1967	9039	1973

Table 3. The number of double cross hybrids and the inbred background of the four parents of the hybrids discussed by Anderson (1944).

	Number and background of inbreds		
Number of hybrids	Reid	Lancaster	Krug
3	3	1	0
1	2	1	1
1	2	0	2
1	4	0	0

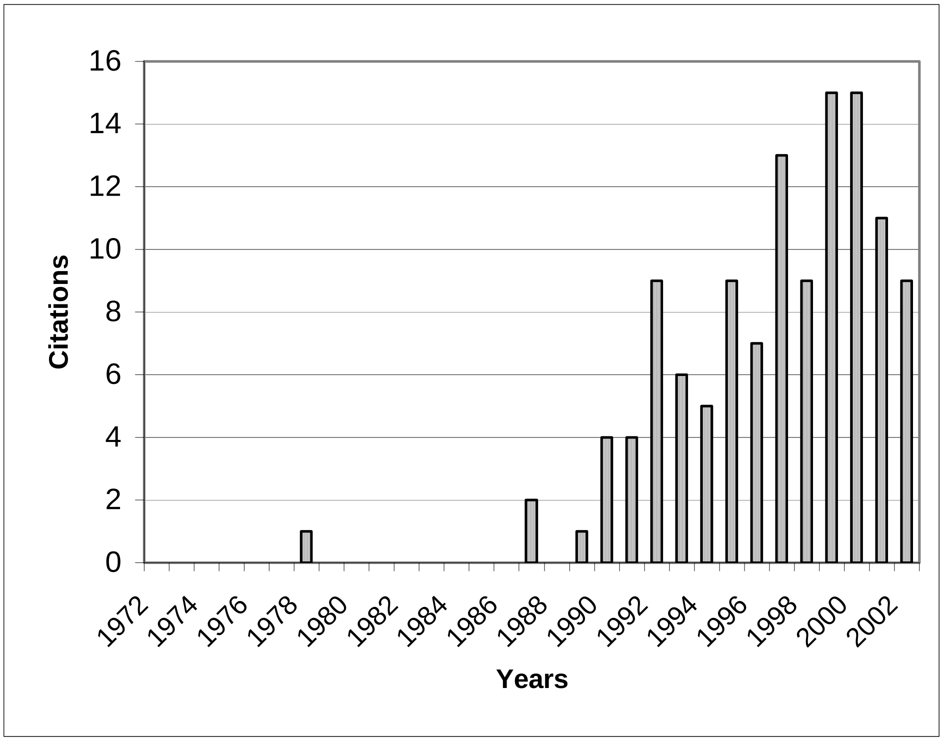

Figure 1. Number of citations per year from a search for the key words “heterotic groups” on the CAB database. Database for 1972-2002 inclusive. Search done in August 2003.

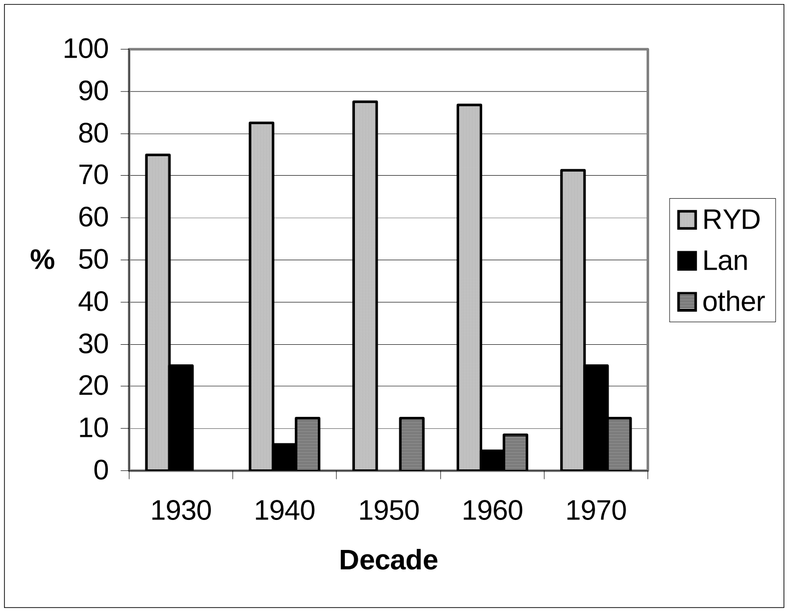

Figure 2. Percent contribution of Reid Yellow Dent (RYD), Lancaster Surecrop (Lan), or other OPVs to the inbred parents of four popular Iowa hybrids per decade from the Russell era studies (Russell, 1974). Reid Yellow Dent includes Stiff Stalk Synthetic inbreds.

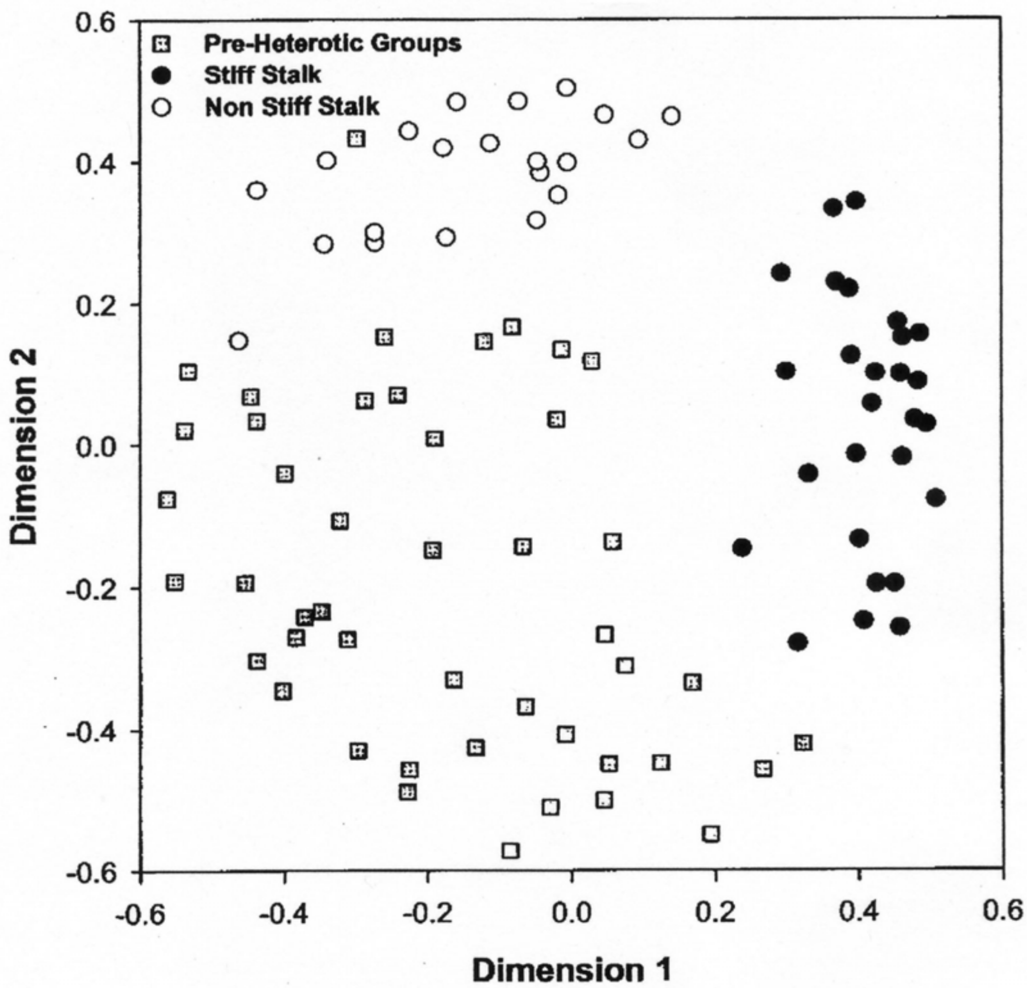

Figure 3. Scores for 94 inbreds contributing to the Era hybrids on the first two dimensions of the multi-dimensional scaling analysis of the SSR polymorphism data for 298 SSR loci (R2 = 0.45 for the two dimension model). (Duvick et al. 2004)