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Similarities among a group of elite maize inbreds as measured by pedigree, F_1 grain yield, grain yield, heterosis, and RFLPs

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Summary. Genetic distances were calculated among 37 inbred lines representing a wide range of related and unrelated elite Corn Belt germ plasm of maize (*Zea Mays* L.), using 257 probe restriction enzyme combinations. Genetic distances based on RFLP data were highly correlated with coefficients of parentage among pairs of lines. The RFLP-based distance had a higher correlation with single-cross grain yield performance and grain yield heterosis than any of the other measures of similarity we calculated using these same lines. The coefficients of determination (r^2) from regressing the coefficient of parentage, grain yield, and grain yield heterosis on Nei's measure of genetic similarity based on RFLP data were 0.81, 0.87 and 0.77, respectively. A cluster diagram based upon the RFLP data grouped the lines into families consistent with the breeding history and heterotic response of these lines. We believe that measures of similarity calculated from RFLP data, coupled with pedigree knowledge and using molecular markers to locate quantitative trait loci (QTL), could allow maize breeders to predict combinations of lines that result in high-yielding, single-cross hybrids.

Key words: *Zea Mays* L. Restriction fragment length polymorphisms – Nei's distance – Coefficient of parentage

Introduction

Soon after the early inbreeding studies with maize (*Zea Mays* L.) by Beal (1880) and Shull (1908), breeders noted that there was a relationship between grain yield or grain yield heterosis and genetic diversity. Empirical studies by Moll et al. (1962, 1965) and Paterniani and Lonnquist (1963) showed a positive relationship between genetic distance, as measured by geographical distance, and both F_1 grain yield and grain yield heterosis in maize. The studies indicated that the amount of heterosis measured between crosses of populations and races from different geographical regions increased as the genetic distance between populations increased. These studies confirmed what breeders had learned through experience, although differences in the adaptability of the populations used by Moll et al. (1962, 1965) may have confounded the interpretation of these results. Other investigators have attempted to show a correlation between genetic distance and distances calculated using morphological markers (Smith and Smith 1989) and chromsome knob size or position (Wellausen and Prywer 1954; Moll et al. 1972; Chugtai and Steffensen 1987). However, these studies produced only meager correlations, especially with respect to populations of highly selected, U.S. Corn Belt maize inbreds. Maize breeders, however, continue to recognize the importance of genetic diversity in hybrid development programs and routinely exploit this in the use of lines from different heterotic groups (Hallauer and Miranda 1981).

Beginning in the 1960s with the development of starch gel electrophoresis techniques, isozyme variants have been used as genetic markers to measure and characterize genetic variation in many crops, including maize (Stuber and Moll 1972; Stuber et al. 1980). Several studies have attempted to use isozyme variation to measure genetic diversity among inbreds lines and to examine the relationship between genetic diversity and grain yield (Stuber et al. 1980; Frei et al. 1986; Price et al. 1986; Lamkey et al. 1987; Smith and Smith 1989). In general, diversity or genetic distance, as measured by isozyme differences, has not been a good predictor of grain yield or grain yield heterosis. Frei et al. (1986) found that the

association between genetic distance based on isozymes and yield performance of single-cross hybrids was closest for lines with similar pedigree backgrounds. This relationships, however, would be of only limited practical use in predicting hybrid yields, since high-yielding hybrids are a result of crosses between inbreds that are unrelated by pedigree due to their selection from different heterotic groups (Hallauer and Miranda 1981). The studies by Smith and Smith (1989), in which 31 enzyme loci were examined in 37 elite U.S. Corn Belt inbred lines encompassing a wide range in pedigree relationships, indicated that pedigree relationship was a better predictor than isozyme distance for predicting single-cross yields or heterosis. Pedigree relationship accounted for 81% of the variation among the single crosses, whereas the modified Roger's distance based on isozyme data accounted for only 32% of the variation. Smith and Smith (1989) also looked at diversity based on analysis of zein proteins with HPLC, and found that this association with single-cross yields was much lower than that based on isozymes (i.e., $r^2 = 0.09$).

Several reasons for the poor association between isozymic diversity and hybrid yield have been given. Isozyme diversity, as measured by isozyme loci, may not contribute to heterosis or may not be linked to loci that contribute to heterosis (Hadjinov et al. 1980; Lamkey et al. 1987). In addition, the isozyme loci that can be sampled and that are polymorphic in elite single crosses of maize represent a small fraction of the genotype, and thus might not adequately reflect genetic diversity at the level required to predict performance.

Restriction fragment length polymorphisms (RFLPs) have the potential to overcome many of the limitations associated with isozymes, and have been used to develop a large set of molecular markers that can be used to describe and to characterize germ plasm. In maize, RFLPs have been used to produce linkage maps (Helentjaris et al. 1986; Burr et al. 1988; Hoisington 1986) and are presently used to map both simply and complexly inherited traits. These markers also allow calculation of genetic distances based on more expanded sampling of the genome than was previously possible. Lee et al. (1989) used RFLPs to examine the relationship between RFLP-based distance and single-cross grain yields in maize. Based on their results, they concluded that genetic distances calculated from RFLPs agreed with pedigree information and that RFLP data could be used to assign maize lines to different heterotic pools.

The objectives of this study are to determine the utility of RFLPs to (1) estimate genetic similarities between lines, (2) compare genetic similarities based on molecular markers with pedigree relationships, and (3) examine the association between genetic diversity based on RFLPs and both single-cross grain yields and grain yield heterosis.

Materials and methods

In this study, 37 highly selected, elite inbred lines of maize representing a broad range of diversity in coefficient of parentage (from 0 to 95%) from the central U.S. Corn Belt were used. These same lines were used in earlier studies, and the methods for the collection of performance data including F_1 grain yield and grain yield heterosis have been previously described (Smith and Smith 1989).

For RFLP analysis, DNA was extracted (Saghai-Maroof et al. 1984) from ground, lyopholized leaf tissue taken from a bulk of 20–30, 5- to 7-week old greenhouse-grown plants. For each inbred line, a 5-μg sample of genomic DNA was digested individually with the restriction endonucleases BamH1, EcoRI, and HindIII. Electrophoresis was carried out in a 0.7 or 1% agarose gel in 100 m*M* TRIS-acetate EDTA, pH 8.1, at 40 V for 18–24 h. Two ranks of 25 lanes were run per gel, with a minimum of three molecular-weight marker lanes per comb; no sample lane was more than five lanes from a molecular-weight standard lane. The molecular-weight marker lanes comprised lambda fragments of 2.0, 2.3, 3.7, 4.4, 4.7, 6.6, 9.4, and 23.1 kb. DNA was transferred (Southern 1975) to MSI magnagraph nylon membranes.

Southern blots were made by capillary transfer to MSI nylon membranes. Random prime-labeled (Feinberg and Vogelstein 1983), isolated maize DNA insert probes were hybridized to maize genomic DNA on the membrane overnight at 65–67 °C (Helentjaris et al. 1986). Post hybridization treatments were three 1-h washes with 0.1% SCP/SDS at 65–69 °C.

Probes employed were supplied by Ben Burr (Brookhaven National Laboratory, designated as BNL) or Dave Hoisington (University of Missouri-Columbia, designated as UMC), or they were selected at Pioneer Hi-Bred International, Inc. (designated as PIO). All probes were derived from genomic maize DNA digested with the methylation-sensitive restriction enzyme PstI. Probes were chosen so as to provide several markers on each of the 20 chromosome arms (Fig. 1).

Following exposure of membranes to film, profiles for inbreds were recorded for each probe/enzyme combination by assigning a number to each band according to its approximate migration distance. Bands were considered different when their range on a gel did not overlap, i.e., if the position of band A across the lanes did not overlap with the position(s) of B. Not all restriction digests were hybridized with all probes; a subset of the total number of restriction enzyme digest by probe combinations were chosen, based on informativeness with respect to a set of 12 previously evaluated inbred lines (Smith et al. 1989).

Bands for each inbred profile from the autoradiograms were coded 1 for presence or 0 for absence of the band. Genetic similarities were then calculated between pairs of lines based on the method developed by Nei and Li (1979), i.e.,

$$D(XY) = N(XY)/[N(X)+N(Y)]$$

where $D(XY)$ is the measure of genetic similarity between a pair of lines, $N(XY)$ is the number of bands common to lines X and Y, and $N(X)$, $N(Y)$ is the number of bands for lines X and Y, respectively.

Cluster diagrams were constructed using the average linkage algorithm in the clustering procedure of SAS for the RFLP data, and using one minus the coefficient of parentage for pedigree data.

Regressions of genetic dissimilarity on coefficients of parentage, F_1 yield, and heterosis were calculated. In addition, the similarities between parents and offspring were calculated for 12 derived lines for which both parents also were included in this study. The F_1 yield and heterosis data have been published in an earlier study (Smith and Smith 1989). Briefly, the F_1 and

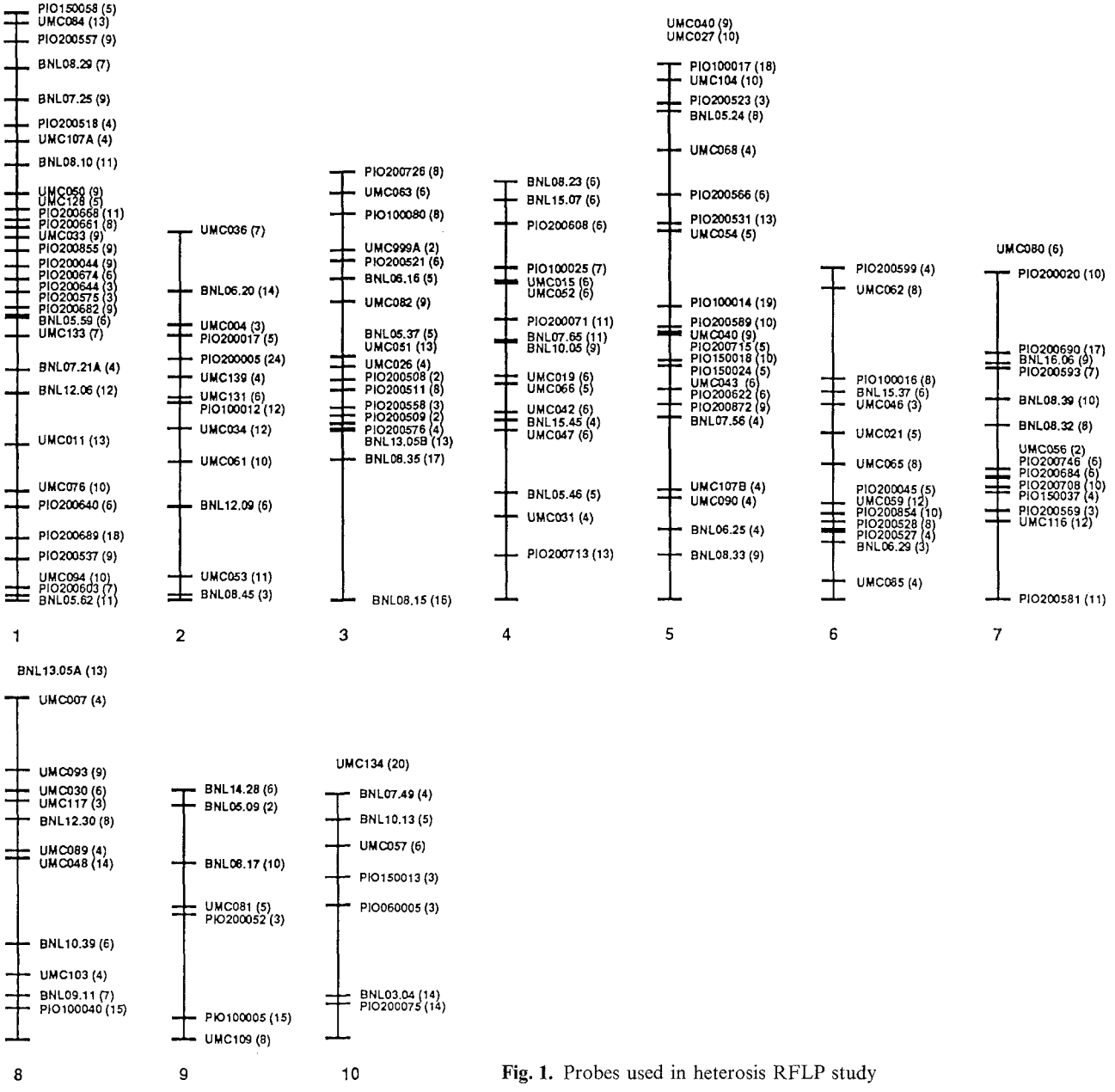

Fig. 1. Probes used in heterosis RFLP study

F_2 generations were grown for 123 crosses between parents, with a coefficient of parentage ranging from 0 to 0.95 (maximum value = 1.00). Sixty-six of the crosses were from a half-diallel among 12 lines. The rest of the crosses were included to extend the range of the coefficient of parentage among the lines used. These materials were grown in four and three locations in the central Corn Belt in the U.S. in 1985 and 1986, respectively. The degree of heterosis (percent) was calculated as twice the difference between the F_1 and F_2 generations divided by the mean of the F_1 times 100. Pedigree distances between lines were calculated as coefficients of parentage (Falconer 1960), in which it was assumed that lines that had no pedigree relationship had a coefficient of parentage of zero, and that lines derived directly from the population Iowa Stiff Stalk Synthetic (BSSS) had a coefficient of parentage of 0.125 (this value was used based on heterosis exhibited by inter- and intraline crosses from several different populations).

Results and discussion

The cluster analysis based on the pedigree data (Fig. 2) assigned each of the 37 inbreds into one or the other of two major groups. One cluster included (non exclusively) the lines derived from, or related to Iowa Stiff Stalk Synthetic (referred to as Stiff Stalk lines, see also Table 1). The other cluster included only non-Stiff Stalk lines. Several line pairs had a default coefficient of parentage of zero simply because no pedigree relationship between these lines is known (Table 1). The assumption of zero for a coefficient of perentage value for pairs with no known pedigree relationship does not imply lack of relationship, only that from our records identity by descent values for

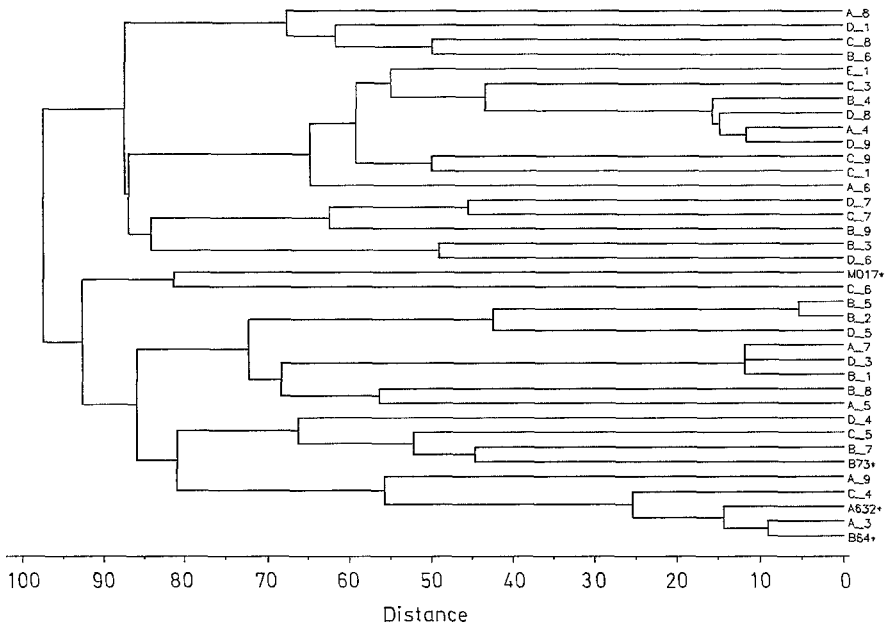

Fig. 2. Dendrogram based on pedigree data

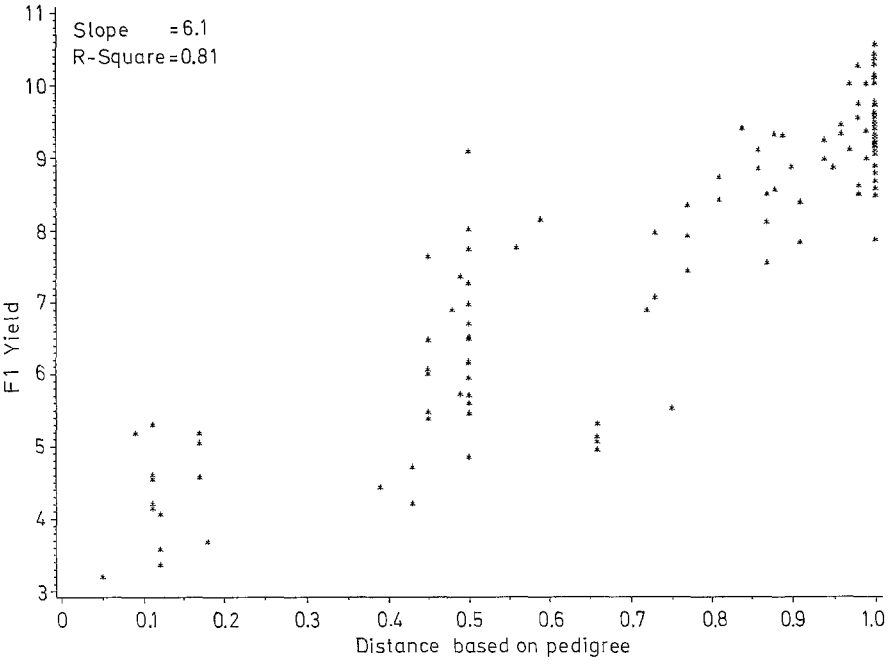

Fig. 3. Plot of F_1 yield versus distance based on pedigree

pairs of alleles involving these parents cannot be calculated. Alleles may, however, be identical in function or due only to probe hybridization region. The lines used in this study were either developed from different heterotic pools (i.e., BSSS and Lancaster) or were from subgroups of the same heterotic group (i.e., families labeled D9 or D7). Lines assigned into different subgroups on the basis of pedigree data reacted accordingly in hybrid combination based on the amount of observed heterosis.

Use of pedigree information thus allows the classification of lines into families. However, these data do not allow good estimation of heterotic response between families. For example, the pedigree data loosely clustered MO17 with the Stiff Stalk group. The line MO17 clustered loosely with the Stiff Stalk lines, which is inconsistent with the well-known performance of MO17 in crosses with Stiff Stalk lines. However, the information on the background of the lines included in this study (Table 1) indicated that several of the Stiff Stalk lines had Lancaster germ plasm in their pedigree, as did the non-Stiff Stalk lines. The distances between lines based on pedigree records were expected to be only approximate, since these calculations assumed equal contribution from each parent and zero coefficients of parentage between lines

Table 1. Coefficient of parentage with the common parent families of lines. Background information for the 39 lines used in the heterosis and RFLP fingerprinting studies

Line	Background		
P_B64	BSSS 87.5%,	41.250B 12.5%	
A_3	BSSS 90.7%, CUSCO <0.1%	41.250B 6.3%,	MINN13 3.1%,
P_A632	BSSS 93.8%,	MINN13 6.3%	
C_4	BSSS 89.2%, CUSCO <0.1%	LANC 6.3%,	MINN13 4.6%,
A_9	BSSS 46.9%, PURYELDENT 10.2%, A109 1.6%,	IODENT 19.4%, MINN13 7.8%, A78 1.6%,	LLE 10.2%, TROYERREID 2.6% CUSCO <0.1%
P_B73	BSSS 100.0%		
B_7	BSSS 93.8%	41.250B 6.3%	
C_5	BSSS 90.6%,	LANC 6.3%,	41.250B 3.1%
D_4	BSSS 50.0%, SRS303 6.3%, OS426 3.1%, OS420 3.1%, LLE 1.6%, TROYERREID 0.4%	DEKALB56 6.3%, F3 5.9%, LANC 3.1%, WM8 3.1%, PURYELDENT 1.6%	MINN13 6.3%, IODENT 4.3%, LF5 3.1%, A48 1.6%, LE 0.4%,
A_5	BSS 50.0%, OS420 12.5%	ALBRTFLINT 25.0%,	OS426 12.5%,
B_8	BSSS 87.5%,	U1210 6.3%,	SD105 6.3%
B_1	BSSS 68.8%, LLE 1.6%,	41.250B 25.0%, PURYELDENT 1.6%,	IODENT 2.7%, TROYERREID 0.4%
D_3	BSSS 68.8%, LLE 1.6%,	41.250B 25.0%, PURYELDENT 1.6%,	IODENT 2.7%, TROYERREID 0.4%
A_7	BSSS 68.8%, LLE 1.6%,	41.250B 25.0%, PURYELDENT 1.6%,	IODENT 2.7%, TROYERREID 0.4%
D_5	DDRF101 50.0%,	BSSS 37.5%,	LANC 12.5%
B_2	BSSS 53.1%, LANC 6.3%, PURYELDENT 0.8%,	DDRF101 25.0%, IODENT 1.4%, TROYERREID 0.2%	41.250B 12.5%, LLE 0.8%,
B_5	BSSS 53.1%, LANC 6.3%, PURYELDENT 0.8%,	DDRF101 25.0%, IODENT 1.4%, TROYERREID 0.2%	41.250 12.5%, LLE 0.8%,
C_6	BSSS 37.5%,	LANC 37.5%,	M3204 25.0%
P_MO17	KRUG 50.0%,	LANC 50.0%	
D_6	FC 50.0%, OS426 6.3%,	LANC 25.0%, FNK1786A 6.3%,	OS420 6.3%, OS420 6.3%
B_3	FC 25.0%, DEKALB56 6.3%, SRS303 6.3%, OS420 3.1%, WM8 3.1%, PURYELDENT 1.6%,	LANC 15.6%, MINN13 6.3%, F3 5.9%, FNK176A 3.1%, A48 1.6%, LE 0.4%,	OS426 6.3%, OS420 6.3%, IODENT 4.3%, LF5 3.1%, LLE 1.6%, TROYERREID 0.4%
B_9	PROCOMP 50.0%, SRS303 6.3%, OS426 3.1%, OS420 3.1%, LLE 1.6%, TROYERREID 0.4%	DEKALB56 6.3%, F3 5.9%, LANC 3.1%, WM8 3.1%, PURYELDENT 1.6%,	MINN13 6.3%, IODENT 4.3%, LF5 3.1%, A48 1.6%, LE 0.4%,
C_7	IODENT 23.7%, MINN13 10.9%, F3 5.9%, LF5 3.1%, TROYERREID 3.0%, A48 1.6%,	LLE 11.7%, DEKALB56 6.3%, OS426 3.1%, OS420 3.1%, A109 1.6%, LE 0.4%,	PURYELDENT 11.7% SRS303 6.3%, LANC 3.1%, WM8 3.1%, A78 1.6%,
D_7	DEKALB 12.5%, F3 11.7%, LANC 6.3%, WM8 6.3%, PURYELDENT 3.1%,	MINN13 12.5%, IODENT 8.6%, LF5 6.3%, A48 3.1%, LE 0.8%,	SRS303 12.5%, OS426 6.3%, OS420 6.3%, LLE 3.1%, TROYERREID 0.8%
A_6	BSSS 50.0%, PURYELDENT 10.2%, A109 1.6%,	IODENT 19.4%, MINN13 4.7%, A78 1.6%	LLE 10.2%, TROYERREID 2.6%,
C_1	FC 25.0%, LLE 10.2%, OS420 3.1%, OS420 3.1%, A78 1.6%	IODENT 19.4%, PURYELDENT 10.2%, OS426 3.1%, TROYERREID 2.6%,	LANC 12.5%, MINN13 4.7%, FNK176A 3.1%, A109 1.6%,
C_9	FC 25.%, LLE 10.2%, OS420 3.1%, OS420 3.1%, A78 1.6%	IODENT 19.4%, PURYELDENT 10.2%, OS426 3.1%, TROYERREID 2.6%,	LANC 12.5%, MINN13 4.7%, FNK176A 3.1%, A109 1.6%,
D_9	IODENT 38.7%, MINN13 9.4%, A78 3.1%,	LLE 20.3%, TROYERREID 5.1%,	PURYELDENT 20.3%, A109 3.1%,
A_4	IODENT 38.8%, MINN13 11.7%, A78 2.3%	LLE 19.9%, TROYERREID 5.0%,	PURYELDENT 19.9%, A109 2.3%,
D_8	IODENT 38.8%, MINN13 11.7%, A78 2.3%	LLE 19.9%, TROYERREID 5.0%,	PURYELDENT 19.9%, A109 2.3%,
B_4	IODENT 38.8%, MINN13 11.7%, A78 2.3%	LLE 19.9%, TROYERREID 5.0%,	PURYELDENT 19.9%, A109 2.3%,
C_3	IODENT 29.1%, FC 12.5%, TROYERREID 3.7%, A109 1.6%,	LLE 14.8%, MINN13 9.4%, ILLONG 3.1%, A78 1.6%	PURYELDENT 14.8%, MDDENT 6.3%, ILLTWOEAR 3.1%,
E_1	FC 25.0%, LLE 10.2%, ILLTWOEAR 6.3%, A109 1.6%,	IODENT 19.4%, PURYELDENT 10.2%, MINN13 4.7%, A78 1.6%	MDDENT 12.5%, ILLONG 6.3%, TROYERREID 2.6%,
B_6	FC 50.0%, ILLTWOEAR 12.5%	MDDENT 25.0%,	ILLONG 12.5%,
C_8	FC 25.0%, ILLONG 6.3%, SRS303 6.3%, OS426 3.1%, OS420 3.1%, LLE 1.6%, TROYERREID 0.4%	MDDENT 12.5%, ILLTWOEAR 6.3%, F3 5.9%, LANC 3.1%, WM8 3.1%, PURYELDENT 1.6%,	DEKALB56 6.3%, MINN13 6.3%, IODENT 4.3%, LF5 3.1%, A48 1.6%, LE 0.4%,
D_1	FC 25.0%, LLE 9.4%, ILLONG 6.3%,	IODENT 19.5%, MINN13 9.4%, ILLTWOEAR 6.3%,	MDDENT 12.5%, PURYELDENT 9.4%, TROYERREID 2.4%
A_8	FC 25.0%, A78 12.5%, ILLTWOEAR 6.3%	HT4 25.0%, MDDENT 12.5%,	A109 12.5%, ILLONG 6.3%,

P_ = Public lines; FC = Pioneer female synthetic; MDDENT = Midland yellow dent; ILLONG = Illinois long ear; ILLTWOEAR = Illinois 2-ear; PURYELDENT = Purdue yellow dent; LANC = Lancaster sure crop; DDRF101 = Pioneer disease synthetic; ALBRTFLINT = Alberta flint; PROCOMP = Pioneer prolific composite

unconnected by pedigree records. The closer the lines were related, the more precise the coefficient of parentages were expected to be. As the distance between clusters approached 0.65–0.70, this measure of relatedness was based upon very imprecise pedigree information. Conversely, pedigree information could be expected to provide a more precise portrayal of distances when there was close association by pedigree, especially in lines involving backcrossing to a recurrent parent.

Distances between lines calculated from the coefficient of parentage were regressed on F_1 grain yields and on grain yield heterosis (Figs. 3 and 4) producing *r*-squared values of 0.81 and 0.72, respectively. Although a large proportion of the variation in grain yield for the hybrids in this study was accounted for by the coefficient of parentage, the deviations from the regression line were significant. The highest yielding crosses were between inbred pair with a coefficient of parentages of zero. Therefore, the coefficient of parentage does not explain any of the grain yield variation in these crosses. Coefficients of parentage simply quantify consanquinity between lines and families of lines having known pedigree relationships. These crosses are not of primary interest since they are not the highest yielding. Pedigree information in this context is only helpful in deciding which crosses not to make.

The 157 DNA probes used in this study were distributed over the genome as indicated in Fig. 1. The map locations of these probes were determined by linkage analysis of F_2 data from other studies conducted at Pio-

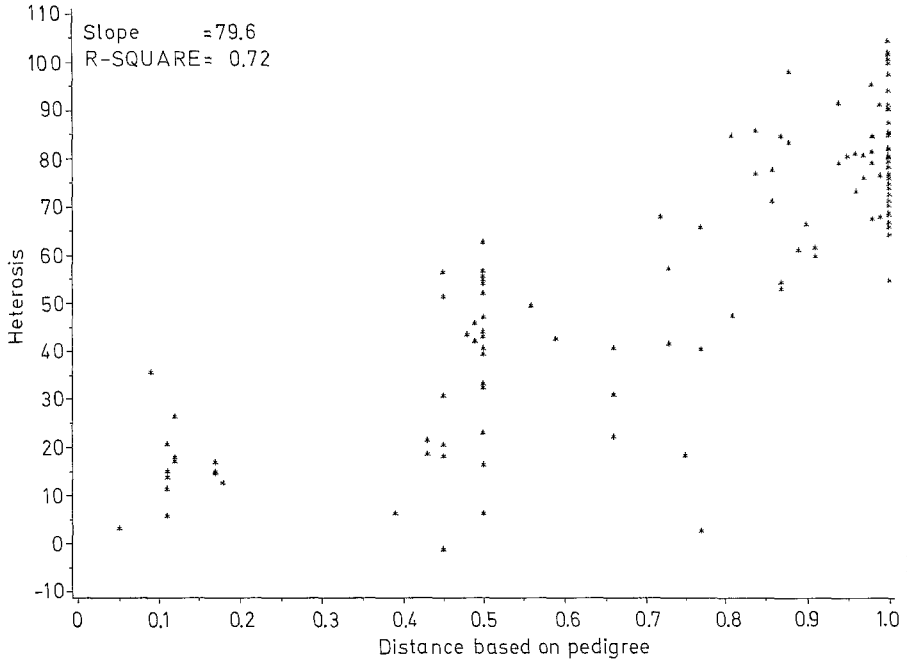

Fig. 4. Plot of heterosis versus distance based on pedigree

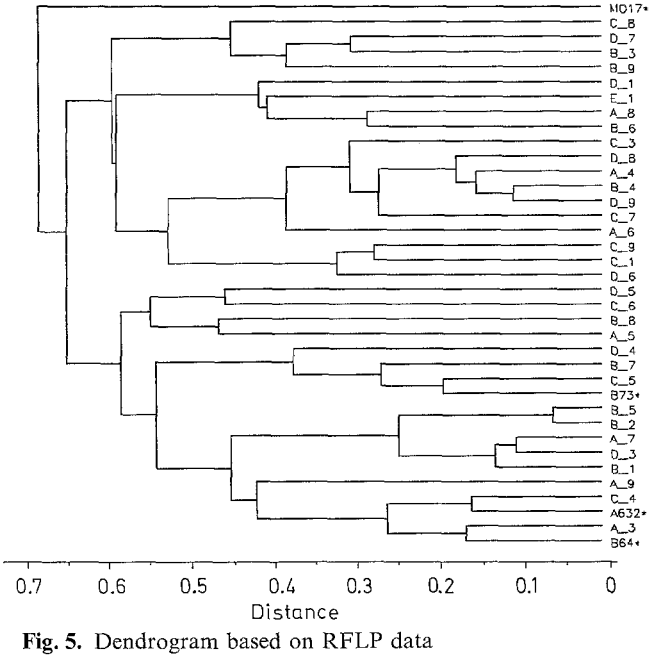

Fig. 5. Dendrogram based on RFLP data

neer Hi-Bred International, Inc. (D. Grant, personal communication) or, for the probes not located to a position on the chromosome (Fig. 1), from mapping data supplied to us with the probe (Hoisington 1986; Burr et al. 1988). Consequently, these chromosome locations are tentative since only some of the observed bands have been mapped using segregation data. Furthermore, in some of the probes DNA hybridization produced multiple (two to four) bands for a number of lines, suggesting the possibility of binding sequence repetition in the genome. The 257 probe by restriction enzyme combinations resulted in a total of 1,205 bands across all inbreds. The number of bands per probe varied from 2 to 20, with some of the restriction enzyme probe combinations resulting in multiple bands. The coverage of the genome based on these probes is adequate, but in the future it would be more efficient to determine a smaller set of probes that will give accurate genetic distances and that are predictive of field performance. Some bands did not segregate in Mendelian fashion, based on the genotypes of parent/progeny combinations. Though the frequency of this aberration was rare, if these probe/restriction enzyme combinations are to be used in the future, the genetic basis of these anomalies needs to be clarified. The calculations of genetic distances stand unaffected, though, since these distances calculated are based simply on the number of common bands, without regard to segregation pattern.

The use of the RFLPs allowed a differential separation of cross performance, based on dissimilarity between lines in the absence of pedigree relationship (Fig. 6). Other distance measures, i.e., distances based on isozymes or morphological traits, also provide a foundation for discrimination among crosses between lines with no pedigree relationship, but these distances are poorly correlated with grain yields and heterosis (Smith and Smith 1989). The cluster tree based on the RFLP information separated the lines into about the same families as did the pedigree information (Fig. 5). However, the genetic distances between families based on RFLP data include both a measure of identity by descent and identity in state. These distances are also more accurate than those calculated from isozymic data, HPLC data, or

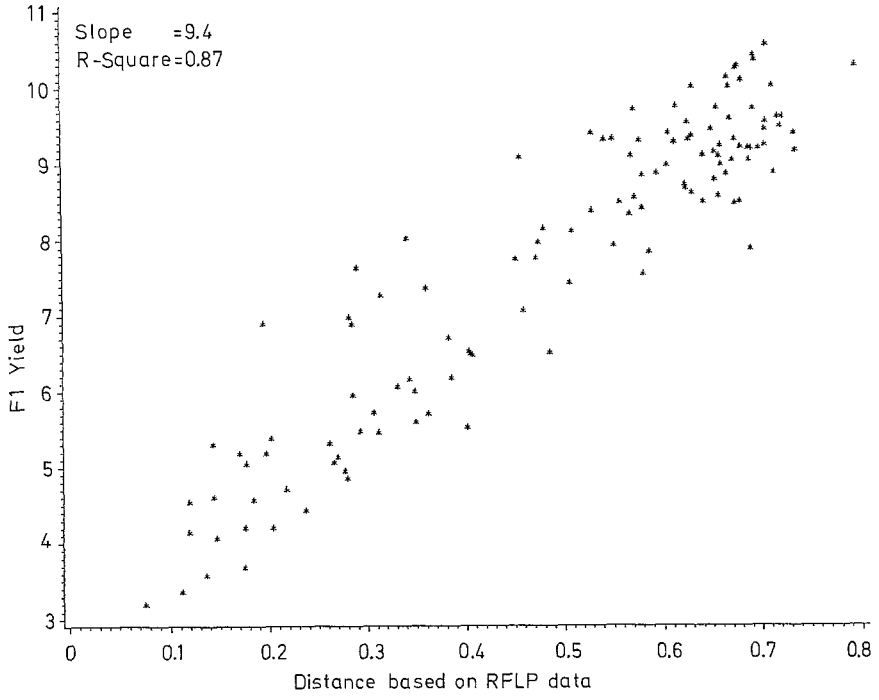

Fig. 6. Plot of F_1 yield versus distance based on RFLP data

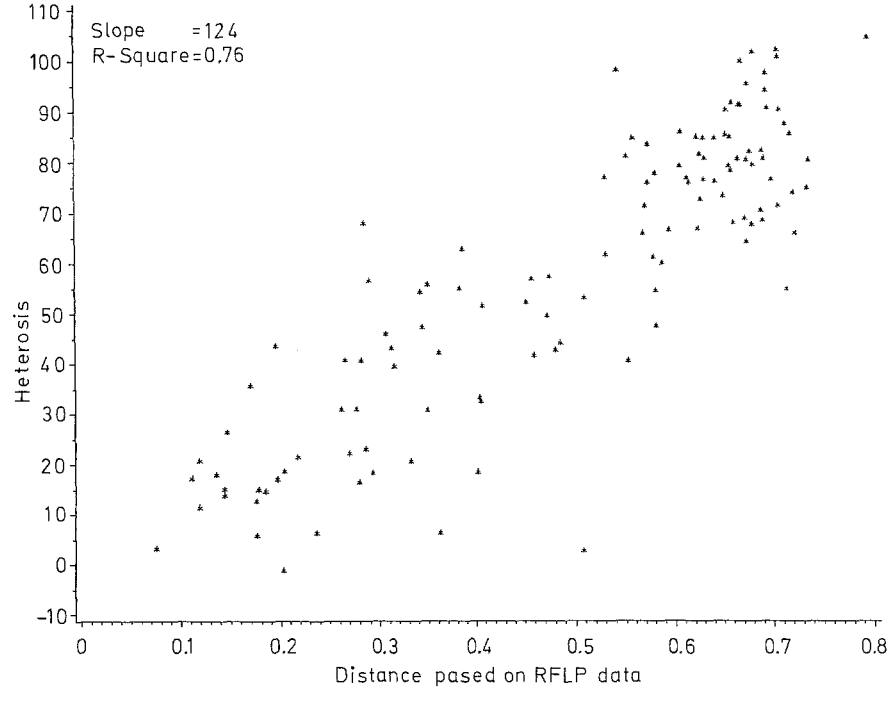

Fig. 7. Plot of heterosis versus distance based on RFLP data

morphological data. This is because RFLP markers provide a more complete sampling of the genome and, on average, greater degree of informativeness per marker. Moreover, in contrast to segregation of morphological traits, RFLP marker classification is uncomplicated by environmental effects.

Based on our knowledge of how these lines were developed and how they perform in crosses, the RFLP data provided similar information on the relative distance between families. The coefficient of determination (r^2) calculated from regression of coefficient of parentage on genetic distance calculated from RFLP data was 0.81, indicating excellent agreement between these two measures of relationship. Genetic distance based on RFLPs accounted for 87% of the variation in the F_1 grain yield and 76% of the variation in grain yield heterosis (Figs. 6 and 7), indicating a strong relationship between RFLP-based genetic distance and grain yield. It also provides a

better prediction of F_1 yield than that provided by the coefficient of parentage, or any of the laboratory (isozyme, zeins) or field-derived (morphology) predictors that we have examined (Smith and Smith 1989).

A significant spread of the points for these crosses around the value for both F_1 grain yield and heterosis predicted by RFLP distance alone is apparent. Several reasons for this spread may be: differential degrees of marker linkage to heterotic loci across the genome; differential expression of heterosis across loci; differential interaction of alleles at the same locus; and the linkage distances between markers and QTL are not constant, and the linkage relationship and QTL effects may change in different inbreds.

In addition, some of the marked chromosome regions could be more important than others in their contribution to F_1 yield and yield heterosis. If quantitative estimates of heterotic effects of probe polymorphisms could be obtained, a linear function with a high degree of predictive precision might be a possibility. Additional information from studies designed to map loci affecting QTL may allow such a weighting of the markers.

The prediction of high-yielding crosses is not yet as precise as it needs to be for routine practical usage in breeding programs. However, information from other studies using molecular markers to locate QTL and other agronomic traits for grain yield can be used to further increase the predictive power of genetic markers. RFLP data should, therefore, allow breeders not only to assign lines to heterotic pools, but they should also be useful for predicting high-yielding crosses.

Prediction of hybrid performance aside, many breeding crosses are made between lines within heterotic pools. The RFLP data will help breeders in choosing breeding crosses by identifying lines that are either very similar or different within the pools. The markers may allow identification of linkage blocks that are responsible for the performance of a given trait within a heterotic pool. Breeders could then look at the fingerprints of derived lines from breeding crosses and save those with particular linkage blocks intact.

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