

1989

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M. Lee

Iowa State University, mlee@iastate.edu

E. B. Godshalk

U.S. Department of Agriculture

K. R. Lamkey

Iowa State University, krlamkey@iastate.edu

W. W. Woodman

Iowa State University

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Abstract

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Disciplines

Agricultural Science | Agronomy and Crop Sciences | Cell Biology | Molecular Genetics | Plant Breeding and Genetics

Comments

This article is published as Lee, M., E. B. Godshalk, Kr R. Lamkey, and W. W. Woodman. "Association of restriction fragment length polymorphisms among maize inbreds with agronomic performance of their crosses." *Crop Science* 29, no. 4 (1989): 1067-1071. doi: [10.2135/cropsci1989.0011183X002900040050x](https://doi.org/10.2135/cropsci1989.0011183X002900040050x). Posted with permission.

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CELL BIOLOGY & MOLECULAR GENETICS

Association of Restriction Fragment Length Polymorphisms among Maize Inbreds with Agronomic Performance of Their Crosses

M. Lee,* E. B. Godshalk, K. R. Lamkey, and W. W. Woodman

ABSTRACT

Restriction fragment length polymorphisms (RFLPs) have been suggested as molecular markers to facilitate improvement of agronomic traits in maize (*Zea mays* L.). The objective of this study was to evaluate the utility of RFLP data in elucidating heterotic patterns among maize lines. Eight maize inbred lines and their 28 single-cross hybrids were evaluated for grain yield at two Iowa locations in each of 2 yr in a randomized-complete block design. The diallel mating design permitted estimation of general and specific combining ability effects. Restriction fragment length polymorphism analysis of inbred lines included five restriction enzymes and five cDNA and 28 genomic clones distributed over the maize genome. Restriction fragment length polymorphism patterns of crosses were predicted from analysis of the inbred parents. Genetic distances between inbred lines were estimated as modified Rogers' distance (MRD). Grain yield and specific combining ability were significantly correlated with MRD for six of the 10 chromosomes. Dispersion of inbred lines and hybrids for RFLP allele frequencies was generally consistent with expectations based on known pedigrees. Results from this study suggest RFLP analysis as a potential alternative to field testing when attempting to assign maize inbred lines to heterotic groups.

A PRIMARY OBJECTIVE in maize breeding programs has been to identify inbred lines that produce crosses exhibiting optimal levels of heterosis. The positive correlation between midparent heterosis of F_1 generation progeny and parental genetic divergence has been demonstrated (Moll et al., 1962, 1965; Paterniani and Lonnquist, 1963). However, Moll et al. (1965) also reported that heterosis actually decreases beyond a certain level of genetic diversity. They attributed this reduction in heterosis to incompatible gene combinations that result when two highly divergent parental populations are crossed.

Moll et al. (1965) defined genetic divergence of two varieties as a function of their ancestry, geographical separation, and adaptation to differing environments. Genetic diversity has also been estimated from isozyme data. Goodman and Stuber (1983) estimated genetic distance from isozyme data collected on 31 races of maize native to Bolivia. Genetic distance estimates, computed as modified Rogers' distance [(MRD) Rogers, 1972], indicated that isozymic variation among the races was consistent with available pedigree information.

Studies have been made to relate isozyme hetero-

zygosity to heterosis in maize. Price et al. (1986) collected field data on single-cross hybrids produced from 48 inbred lines. Genotypes of the crosses were inferred from parental inbred genotypes at 13 polymorphic isozyme loci. They found cross performance to be unrelated to allelic differences among the inbred lines at the 13 isozyme loci studied. Lamkey et al. (1987) also studied the relationship between allelic differences at enzyme loci and cross performance in maize. Data collected at 11 isozyme loci on 24 high-yielding lines and 21 low-yielding lines indicated that allelic differences between inbred lines were not predictive of hybrid performance. Hunter and Kannenberg (1971) and Heidrich-Sobrinho and Cordeiro (1975) found that specific combining ability (SCA) of maize grain yield was uncorrelated to heterozygosity at the isozyme loci. Frei et al. (1986) reported that isozyme dissimilarity was more predictive of maize yield when restricting analysis to inbred lines with similar pedigrees.

Restriction fragment length polymorphisms (RFLPs) have been proposed as an additional approach to detecting molecular genetic polymorphisms in plant species. A major advantage provided by RFLPs in maize is the potentially unlimited number of loci and alleles per locus. Burr et al. (1983) suggested the use of RFLPs in estimating genetic diversity, mapping genes that control quantitatively inherited traits, and selecting for increased heterozygosity or homozygosity. Given these potential uses of RFLPs, the objective of this study was to evaluate the potential of RFLPs for assigning maize inbred lines to heterotic groups.

MATERIALS AND METHODS

Twenty-eight maize single crosses were produced from a diallel mating of the inbred lines: B70, B73, B77, B79, B84, Mo17, N28, and Va35. Three of these lines (B73, B84, and N28) were derived from 'Iowa Stiff Stalk Synthetic' (BSSS), and three (B70, Mo17, and Va35) were descended from the inbred C103. The remaining two lines, B77 and B79, were derived from synthetics BS11 (Hallauer et al., 1974) and BS10 (Russell et al., 1971), respectively. The inbred B77 combines well with BSSS inbreds and B79 combines well with C103-derived inbreds (W.A. Russell, personal communication, 1988).

The eight inbreds and 28 crosses were evaluated for grain yield (Mg ha^{-1}) at two Iowa locations (Ames and Kanawha) in 1984 and 1985. The experimental design was a randomized-complete block, with three replications at each location in 1984, two replications at Kanawha in 1985, and four replications at Ames in 1985. Plots consisted of three rows that were 5.4 m long, with 0.76 m between rows. Plant densities were approximately 62 000 plants ha^{-1} . Data were collected on the middle row of each plot to reduce competition effects between inbreds and crosses. Plots were machine planted and harvested by hand.

M. Lee and W.W. Woodman, Dep. of Agronomy; E.B. Godshalk and K.R. Lamkey, USDA-ARS and Dep. of Agronomy, Iowa State Univ., Ames, IA 50011. Joint contribution from USDA-ARS and Journal Paper no. J-13113 of the Iowa Agric. and Home Economics Exp. Stn., Ames, IA 50011; Project 2818. Received 27 June 1988. *Corresponding author.

Yield data were analyzed over environments with a model that considered all effects, except replicates and environments, as fixed effects. Single cross and single cross \times environment degrees of freedom and sums of squares were partitioned into sources of variation and interactions with environment due to general combining ability (GCA) and specific combining ability (SCA). This partitioning was in accordance with Griffing's (1956) model I of method 4, in which analysis is restricted to one set of F_1 's and excludes parents and reciprocal F_1 's. This method was preferred because the resulting GCA estimates would not be affected by the substantial differences in between inbred lines and their crosses regarding vigor and grain yield.

The inbreds were analyzed for their respective RFLP patterns. Leaf tissue samples were collected from five seedlings of each inbred grown in a glasshouse under natural light. The samples were lyophilized and equal quantities of tissue from each seedling were bulked for each inbred. The DNA isolation proceeded according to the procedure described by Saghai-Marooof et al. (1984). Five restriction enzymes (BglII, EcoRI, EcoRV, HindIII, and SstI) were used to identify combinations of DNA clones and enzymes that detected polymorphisms among the sample of inbreds used in this study. Upon digestion according to manufacturer's instructions, DNA samples were loaded onto neutral agarose gels, electrophoresed, and transferred from gels to nylon membranes according to the methods described by Helentjaris et al. (1985). Five cDNA and 28 genomic clones were selected from a collection of mapped maize clones provided by T. Helentjaris (Native Plants Inc., Salt Lake City, UT). The clones were selected on the basis of their single-copy hybridization patterns (detecting one or two polymorphic fragments per inbred depending on the clone-enzyme combination) and to provide coverage of at least one clone per chromosome arm (Table 1). Linkage information for these clones was obtained from the maize RFLP map published by Helentjaris (1987). Clones were radiolabelled to approximately 10^6 cpm/ μ g DNA by random-primer synthesis of isolated inserts (Feinberg and Vogelstein, 1983) and hybridized to DNA fragments located on nylon membranes (Helentjaris et al., 1986).

Restriction fragment length polymorphism allele constitutions were determined for each inbred for each clone-enzyme combination evaluated. Each clone-enzyme combination was considered as a locus. Assignment of allelic designations were based on polymorphisms for each clone-enzyme combination. Inbreds with the same number and location of bands in the autoradiograph for a particular clone-

enzyme combination were assigned the same allelic designation; any change in band location or number received a different allele designation. Restriction fragment length polymorphism patterns of the inbreds did not suggest any evidence of remnant heterozygosity or seed stock contamination. The possibility of remnant heterozygosity within these inbred lines at the loci evaluated can be considered minimal due to the simple banding patterns produced by the selected clones.

Genetic distances among all possible pairs of inbreds were estimated from the modified Rogers' distance [(MRD) Rogers, 1972] equation:

$$MRD = \left[\sum_{k=1}^{334} (p_{ik} - p_{jk})^2 \right]^{1/2} / (2n)^{1/2}$$

where p_{ik} and p_{jk} are frequencies of the k^{th} RFLP allele for the i^{th} and j^{th} inbreds, respectively, and n is the total number of RFLP loci (Rogers, 1972; Wright, 1978). Modified Rogers' distances are interpreted as representing the extent of genetic diversity between two individuals. Genetic diversity is assumed to be directly proportional to the magnitude of the MRD estimate. An MRD value of 0.0 indicates no diversity between a pair of inbreds, whereas a value of 1.0 represents maximum diversity for a given set of loci. Simple correlations were calculated for various combinations of yield means, GCA, SCA, and MRD computed per chromosome and over all chromosomes.

Principal component analyses (PCA) were computed on both inbred and predicted single-cross RFLP allele frequency data to determine if any pattern existed in the data. Each column of data represented an allele for a particular clone-enzyme combination. For example, the matrix for the inbred data had one row for each inbred and 334 columns representing the total number of alleles from all probe-enzyme combinations included in the study. This matrix consisted entirely of 0 and 1's. An analogous matrix was used for the single-cross data except that this matrix could contain 0, 1, and 0.5's representing the two possible parental homozygous classes and the heterozygous class. Principal component analyses for inbreds and predicted single crosses were done on the simple correlation matrices computed from the inbred and single cross RFLP allele frequency matrices, respectively. First and second principal components were plotted to enhance the dispersion of inbreds and single crosses according to their allele frequencies.

RESULTS AND DISCUSSION

The highest single cross grain yields were obtained from the BSSS \times C103 family of crosses (Table 2). Crosses between B79- and C103-derived inbreds also produced high yields. Estimates of positive SCA were greatest for the Mo17 \times B79 and B73 \times Mo17 crosses. Crosses among BSSS-derived inbreds and among C103-derived inbreds resulted in relatively low yields and significant negative SCA estimates. Progeny from crosses involving B77 were also frequently lower in grain yield and estimates of SCA.

The MRD values and predicted number of heterozygous RFLP loci were greater for BSSS \times C103 family of crosses and relatively smaller for comparisons among inbreds within the BSSS and C103 families of crosses when compared to the average for all crosses (Table 2). The B73 \times Va35, N28 \times B70, and N28 \times Va35 crosses had relatively larger MRD esti-

Table 1. Number of clones and restriction fragment length polymorphism (RFLP) alleles associated with each of the 10 chromosomes in the maize genome.

Chromosome	Clone designation†	Clones	Alleles
		no.	
1	238, 258, 429	3	32
2	122, 239, 274, 287	4	44
3	247, 249, 257, 296, 425	5	53
4	270, 284	2	22
5	233, 237, 409	3	23
6	223, 235, 280	3	48
7	112, 113, 263	3	30
8	103, 107, 110, 114	4	21
9	253, 291, 416	3	34
10	264, 285, 437	3	27
Total		33	334

† Clone designations derived from the maize RFLP linkage map (Helentjaris, 1987). Each number corresponds to a clone with a known location on the map.

mates; relatively smaller MRD values were obtained for the B73 × B84 and N28 × B84 crosses when compared to the average for all crosses. These results indicate that genetic diversity, determined from RFLP data of inbred lines and predicted for their crosses, was generally consistent with expectations based on known ancestries of the maize inbreds.

Specific combining ability and MRD were significantly correlated for Chromosomes 1, 2, 3, 5, 7, 10, and over all chromosomes (Table 3). Mean yield of the crosses was significantly or highly significantly positively correlated with MRD of Chromosomes 1, 3, 5, 7, 8, and over all chromosomes. The BSSS × C103 family of crosses had the greatest grain yield and MRD values, and crosses among related lines had the smallest MRD values and grain yield (Table 2). An

Table 2. Mean grain yield, estimated specific combining ability effects, modified Rogers' distance, and predicted number of heterozygous restriction fragment length polymorphism (RFLP) loci of 28 maize single crosses.

Families and crosses	Grain yield	Specific combining ability effect	Modified Rogers' distance	Predicted heterozygous RFLP loci†
				no.
	—Mg ha ⁻¹ —			
BSSS × BSSS‡	7.00	-0.83	0.545	33
N28 × B73	6.97	-0.75**	0.613	41
N28 × B84	6.65	-0.87**	0.542	32
B73 × B84	7.39	-0.87**	0.479	25
C103 × C103	6.92	-1.15	0.636	44
Va35 × B70	7.61	-0.43*	0.606	40
VA35 × Mo17	5.93	-1.65**	0.697	53
B70 × Mo17	7.22	-1.38**	0.606	40
BSSS × C103	8.58	0.63	0.792	68
N28 × Va35	7.64	0.65**	0.801	70
N28 × B70	8.73	0.71**	0.807	71
N28 × Mo17	8.00	0.44*	0.796	69
B73 × Va35	8.34	0.62**	0.824	74
B73 × B70	9.27	0.52*	0.784	67
B73 × Mo17	9.21	0.91**	0.766	64
B84 × Va35	8.18	0.65**	0.790	68
B84 × B70	9.00	0.44*	0.772	65
B84 × Mo17	8.86	0.76**	0.784	67
BSSS × B77	7.44	0.06	0.752	62
B73 × B77	8.10	0.41*	0.729	58
B84 × B77	7.55	0.06	0.760	63
N28 × B77	6.67	-0.29	0.766	64
C103 × B77	7.52	0.02	0.751	62
B70 × B77	7.84	-0.15	0.748	61
Mo17 × B77	7.42	-0.12	0.710	55
Va35 × B77	7.30	0.34	0.796	69
BSSS × B79	7.38	-0.30	0.716	56
B73 × B79	7.16	-0.83**	0.704	54
B84 × B79	7.62	-0.17	0.684	51
N28 × B79	7.36	0.10	0.760	63
C103 × B79	8.19	0.38	0.772	65
B70 × B79	8.59	0.29	0.754	62
Mo17 × B79	8.89	1.04**	0.790	68
Va35 × B79	7.09	-0.19	0.772	65
B77 × B79	6.99	-0.25	0.778	66
LSD (0.05)	0.77§	—	—	—
LSD (0.05, \hat{s}_{ij} vs. \hat{s}_{ik})¶	—	0.62	—	—
LSD (0.05, \hat{s}_{ij} vs. \hat{s}_{kl})¶	—	0.55	—	—

*,** Significantly different from 0.0 at the 0.05 and 0.01 probability levels, respectively.

† A locus represents a clone/enzyme combination. There was a total of 109 loci.

‡ Values on the first line for each family of crosses represent the average of crosses within the family.

§ LSD (0.05) for comparing single cross yield means.

¶ LSD (0.05) for comparing single cross specific combining abilities.

exception to this is the B77 × B79 cross, which had a large MRD value and low yield. In addition, within the BSSS × C103 group, yield tended to decrease as MRD increased as indicated by a correlation between yield and MRD of -0.59. Grain yield and MRD of BSSS × B79 family of crosses were smaller in comparison with values of C103 × B79 family of crosses. These data agree with the known breeding behavior of B79 and suggest that B79 may be more closely related to BSSS germplasm than C103 germplasm.

The molecular and grain yield data suggest that B77 represents a germplasm source unrelated to BSSS and C103-derived lines. Contrary to the performance of BSSS × C103 family of crosses; grain yield and MRD data associated with hybrids of B77 did not conform to a distinct pattern (Table 2). Yield of the BSSS × B77 family of crosses increased as MRD values decreased, whereas yield of C103 × B77 family of crosses did not respond linearly to changes in MRD. In the plot of grain yield vs. MRD (Fig. 1), four of the seven crosses in quadrant 4 involved B77 as a parent. The quadrants are defined by horizontal and vertical lines drawn along the overall mean values for grain yield and MRD, respectively. Crosses in quadrant 4 had below-average grain yield and above-average MRD values. According to Moll et al. (1965), the low grain

Table 3. Simple correlations (N = 28) among grain yield, estimated specific combining ability (SCA), and modified Rogers' distance (MRD) for maize crosses.

	Grain yield	SCA
MRD		
Chromosome 1	0.404*	0.567**
Chromosome 2	0.125	0.490**
Chromosome 3	0.491**	0.650**
Chromosome 4	-0.028	0.240
Chromosome 5	0.428*	0.781**
Chromosome 6	0.299	0.367
Chromosome 7	0.603**	0.711**
Chromosome 8	0.510**	0.349
Chromosome 9	0.251	0.207
Chromosome 10	0.024	0.413*
All Chromosomes	0.462*	0.737**

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

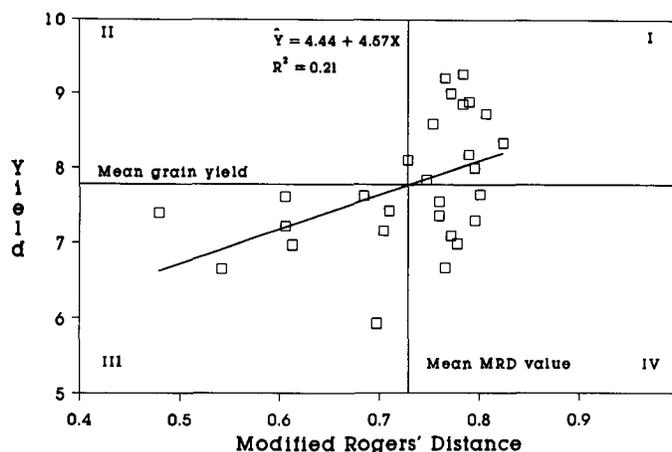


Fig. 1. Plot of single-cross grain yield (Mg ha⁻¹) vs. modified Rogers' distance (MRD) estimates. The horizontal and vertical lines delineating the quadrants are located at the mean values for the respective axes.

yield may be the result of deleterious gene combinations from the two inbred parents. The remaining 21 crosses were located in quadrants 1 and 3, implying a relation of increases in yield to increases in genetic distance for those crosses.

Principal component analysis was performed on single-cross RFLP allele frequencies to examine the correspondance between the dispersion pattern of crosses (based on predicted allele frequencies) and their agronomic performance (Fig. 2). The first and second components accounted for 26.0 and 18.9%, respectively, of the total variance. Clustering of the crosses for predicted RFLP allele frequencies was consistent with their known heterotic groups. Six distinct groups resulted, with the BSSS \times C103, B77 \times B79, and C103 \times B79 crosses collectively forming one group. The 15 remaining crosses segregated into five groups (i.e., BSSS \times BSSS, BSSS \times B77, BSSS \times B79, C103 \times C103, and C103 \times B77).

Principal component analysis of inbred RFLP allele

frequencies was done to observe similarities among the inbreds for their respective allele frequencies. The first principal component accounted for 25.8% of the total variation, and the second component accounted for 18.8%. First and second components of the eight inbreds were plotted (Fig. 3) and clustering of the inbreds into groups was consistent with expectations. Inbreds with common ancestries had similar RFLP allele frequencies. Both B77 and B79 were approximately intermediate to the BSSS and C103 families, although B77 was somewhat closer to the C103 group of inbreds and B79 was located closer to the BSSS group of inbreds. The three BSSS-derived inbreds (B73, B84, and N28) were more closely clustered, whereas the three C103-derived inbreds were more loosely grouped. Crosses with BSSS-derived inbreds also tended to group more closely than crosses with C103-derived inbreds (Fig. 2). This may reflect a greater degree of relatedness among the BSSS-derived lines than among the C103-derived lines. However, accord-

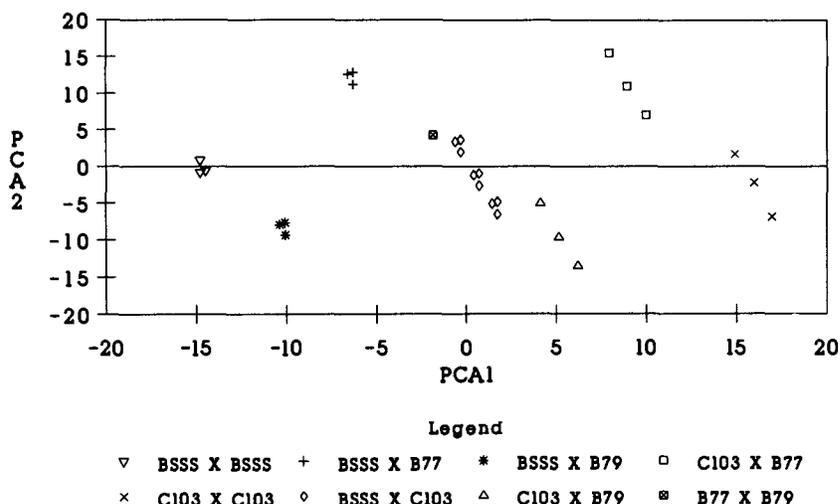


Fig. 2. Plot of the first (Y1) and second (Y2) principal components from analysis of single-cross restriction fragment length polymorphism data. The symbols identify single crosses involving inbreds B77, B79, and BSSS-derived (B73, B84, and N28), and C103-derived (Mo17, B70, and Va35) inbred lines.

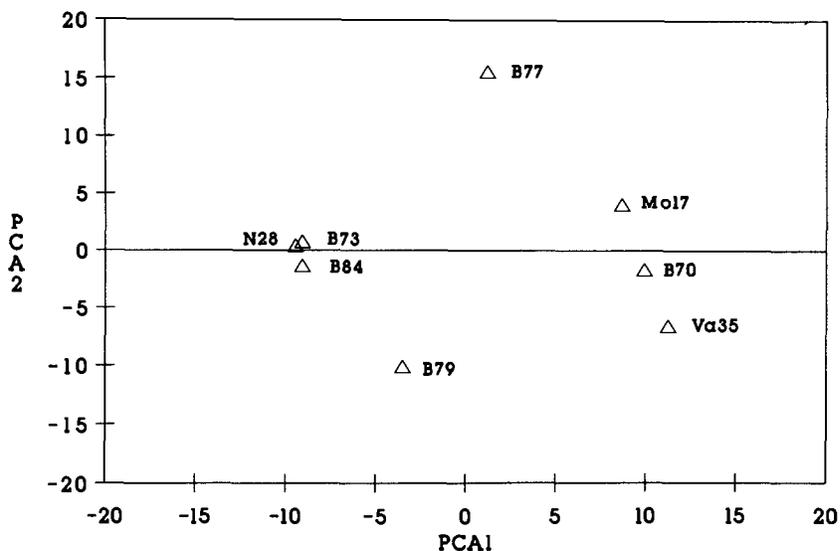


Fig. 3. Plot of the first (Y1) and second (Y2) principal components from analysis of inbred restriction fragment length polymorphism data.

ing to Malecot's coefficients of kinship (Malecot, 1969), the C103-derived lines are more closely related than the BSSS-derived lines. Coefficients of kinship (O.S. Smith, personal communication, 1987), among the C103-derived lines (0.249 for all combinations) were larger than those among BSSS-derived lines (0.125 for B73 and B84; 0.0 for B73 and N28 and for B84 and N28). The discrepancy between coefficients of kinship and diversity based on RFLP data is not readily explained. The coefficients of kinship are only estimates, however, made from complex ancestral patterns among the maize inbreds and do not include the effects of selection. More extensive mapping and analysis of the maize genome may permit better estimates of similarity and, perhaps, identification of more suitable methods to evaluate the degree of kinship.

Results of this study indicate potentially successful utilization of RFLP alleles to assign maize inbreds to their respective heterotic groups and to investigate relationships among inbred lines. Allocation of maize inbreds, of unknown heterotic pattern, to heterotic groups before field testing may allow the breeder the opportunity to reduce costs by avoiding crosses within heterotic groups. Restriction fragment length polymorphism data from a larger set of crosses (compared with the current study) is recommended to describe, with greater precision, the relationship between RFLP-based genetic distance estimates and the heterotic grouping of inbred lines.

ACKNOWLEDGMENTS

We would like to thank O.S. Smith for reading the manuscript. This work was supported by grants from the Iowa State Biotechnology Council and Pioneer Hi-Bred International.

REFERENCES

- Burr, B., S.V. Evola, F.A. Burr, and J.S. Beckman. 1983. The application of restriction fragment length polymorphisms to plant breeding. p. 45-59. *In* J.K. Setlow and A. Hollaender (ed.) Genetic engineering principles and methods. Vol. 5. Plenum Press, London.
- Feinberg, A.P., and B. Vogelstein. 1983. A technique for radiolabeling DNA restriction fragment length polymorphisms to high specific activity. *Anal. Biochem.* 132:6-13.
- Frei, O.M., C.W. Stuber, and M.M. Goodman. 1986. Uses of allozymes as genetic markers for predicting performance in maize single cross hybrids. *Crop Sci.* 26:37-42.
- Goodman, M.M., and C.W. Stuber. 1983. Races of maize. VI. Isozyme variation among races of maize in Bolivia. *Maydica* 28:169-187.
- Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. *Aust. J. Biol. Sci.* 9:463-493.
- Hallauer, A.R., S.A. Eberhart, and W.A. Russell. 1974. Registration of maize germplasm. *Crop Sci.* 14:341-342.
- Heidrich-Sobrinho, E., and A.R. Cordeiro. 1975. Codominant isoenzymic alleles as markers of genetic diversity correlated with heterosis in maize (*Zea mays* L.). *Theor. Appl. Genet.* 46:197-199.
- Helentjaris, T. 1987. A genetic linkage map for maize based on RFLPs. *Trends Genet.* 3:217-221.
- , G. King, M. Slocum, C. Siedenstrang, and S. Wegman. 1985. Restriction fragment polymorphisms as probes for plant diversity and their development as tools for applied plant breeding. *Plant Mol. Biol.* 5:109-118.
- , M. Slocum, S. Wright, A. Schaefer, and J. Neinhuis. 1986. Construction of genetic linkage maps in maize and tomato using restriction fragment length polymorphisms. *Theor. Appl. Genet.* 72:761-769.
- Hunter, R.B., and L.W. Kannenberg. 1971. Isozyme characterization of corn (*Zea mays* L.) inbreds and its relation to single cross hybrid performance. *Can. J. Genet. Cytol.* 13:649-655.
- Lamkey, K.R., A.R. Hallauer, and A.L. Kahler. 1987. Allelic differences at enzyme loci and hybrid performance in maize. *J. Hered.* 78:231-234.
- Malecot, G. 1969. *The Mathematics of Heredity*. Freeman, San Francisco.
- Moll, R.H., J.H. Lonquist, J.V. Fortuna, and E.C. Johnson. 1965. The relation of heterosis and genetic divergence in maize. *Genetics* 52:139-144.
- , W.S. Salhuana, and H.F. Robinson. 1962. Heterosis and genetic diversity in variety crosses of maize. *Crop Sci.* 2:197-198.
- Paterniani, E., and J.H. Lonquist. 1963. Heterosis in interracial crosses of maize (*Zea mays* L.). *Crop Sci.* 3:504-507.
- Price, S.C., A.L. Kahler, A.R. Hallauer, P. Charmley, and D.A. Giegel. 1986. Relationships between performance and multilocus heterozygosity at enzyme loci in single-cross hybrids of maize. *J. Hered.* 77:341-344.
- Rogers, J.S. 1972. IV. Measures of similarity and genetic distance. *Studies in Genetics VII*. Univ. Tex. Publ. 7213:145-153.
- Russell, W.A., L.H. Penny, A.R. Hallauer, S.A. Eberhart, G.E. Scott, W.D. Guthrie, and F.F. Dicke. 1971. Registration of maize germplasm synthetics. *Crop Sci.* 11:140-141.
- Saghai-Marooif, M.A., K.M. Soliman, R. Jorgenson, and R.A. Allard. 1984. Ribosomal DNA spacer length polymorphisms in barley: Mendelian inheritance, chromosomal location, and population dynamics. *Proc. Natl. Acad. Sci.* 81:8014-8018.
- Wright, S. 1978. Evolution and the genetics of populations. p. 79-103. *In* Variability within and among natural populations. Vol. 4. Univ. of Chicago Press, Chicago, IL.