

Evaluation of Theory for Identifying Populations for Genetic Improvement of Maize Hybrids

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ABSTRACT

The ability to identify populations with the greatest chance for breeding success may increase the use of unadapted populations by concentration of resources on favorable germplasm. This study was conducted to evaluate the effectiveness of a method (estimates of $\bar{C}_{pe\mu}$) for identifying maize (*Zea mays* L.) populations with the greatest number of dominant alleles at loci that are homozygous recessive in a single cross. This study also evaluates the effectiveness of a relationship estimator for detecting similarities between a population and the inbreds of a single cross. Estimates of $\bar{C}_{pe\mu}$ and the relationship estimator were calculated by using donor populations of known composition and relationship to the recipient single cross. Six recipient single crosses were formed from the diallel cross of maize inbreds B73, B79, B77, and Mo17. Donor populations were composed of various proportions of inbreds B79 and B77. Estimates of $\bar{C}_{pe\mu}$ correctly identified the population expected to have the largest number of unique dominant alleles in three of five single crosses (60%) for grain yield. For ear height, $\bar{C}_{pe\mu}$ correctly identified the population expected to have the largest number of unique dominant alleles in four or five single crosses (80%). Estimates of $\bar{C}_{pe\mu}$ did not identify populations expected to contain dominant alleles for earlier silking, suggesting that additive gene action or epistasis were important for silking date. The relationship estimator for yield correctly identified the known relationship between the populations and the inbred parents of the single crosses. The successful application of $\bar{C}_{pe\mu}$ to exotic populations is uncertain because of a low frequency of favorable dominant alleles contained by exotics for important economic traits.

THE DEGREE of success attained by a breeding program is a function of the germplasm and breeding procedure. A poor choice of germplasm will limit the success of the breeding program regardless of the breeding procedure (Hallauer and Miranda, 1988). Exotic or unadapted populations may be excellent sources of favorable alleles not currently present in populations used for inbred development (Hallauer, 1978; Brown, 1983). Use of unadapted germplasm would also help increase the genetic diversity among widely grown elite commercial cultivars (Stuber, 1978; Anonymous, 1972; Geadelmann, 1984; Holley and Goodman, 1988). Goodman (1985) reviewed the status of exotic maize germplasm use and attributed the limited success to poor choices of exotic germplasm rather than to the breeding procedures used.

The ability to effectively screen populations to identify those most promising for breeding success may enhance the use of unadapted or exotic germplasm in U.S. maize production. Theory for identifying populations for use in crossing with inbreds of elite single

crosses has been proposed by Dudley (1984, 1987b). Loci Classes *i*, *j*, *k*, and *l* are divisions of the loci controlling the trait of interest and are determined by the single cross to be improved. Loci at Class *i* are homozygous dominant in the single cross. Loci at Classes *j* and *k* are heterozygous, with the dominant allele from parent one designating Class *j* and the dominant allele from parent two designating Class *k*. Class *l* loci are homozygous recessive in the single cross. The most immediate improvement of the single cross is by introgression of dominant alleles into Class *l* loci (Dudley, 1984). Dudley (1984) developed a statistic ($\bar{C}_{pe\mu}$) that is a measure of the frequency of dominant alleles in a population at loci that are homozygous recessive in the single cross to be improved (Class *l* loci). Assumptions used to derive $\bar{C}_{pe\mu}$ include a constant genotypic value (μ) for loci affecting the trait, complete dominance, and no epistasis. Gerloff and Smith (1988) compared $\bar{C}_{pe\mu}$ with other population identification statistics by using computer simulation. In the derivation of $\bar{C}_{pe\mu}$, Dudley (1984) assumed that the frequency of favorable alleles at Class *j* (\bar{p}_j) and *k* (\bar{p}_k) loci in the population was equal. Gerloff and Smith (1988) established that failure of this assumption would decrease the ability of $\bar{C}_{pe\mu}$ to correctly identify populations with the greatest frequency of favorable alleles at Class *l* loci. Dudley (1987b) proposed a modified method of population identification that removes the $\bar{p}_j = \bar{p}_k$ assumption. The modified method also provides a test for determining the relationship between the populations and the parents of the single cross.

Dudley (1987b) compared the modified estimator ($\bar{C}_{pe\mu}$) to $\bar{C}_{pe\mu}$ and other statistics by using computer simulation data generated by Gerloff (1985). Estimates of $\bar{C}_{pe\mu}$ were closest in agreement to the actual superiority measures of the simulated populations. Dudley (1988) evaluated 19 populations for their ability to improve the single cross B73 \times Mo17. The traits measured were grain yield, root lodging, stalk lodging, ear height, and days to pollen shed. For grain yield, 8 of the 19 populations had estimates of $\bar{C}_{pe\mu}$ greater than two times the standard error. Of these eight populations, only one was relatively unselected for combining ability with maize lines adapted to the U.S. Corn Belt. Hogan and Dudley (1991) critically evaluated the ability of $\bar{C}_{pe\mu}$ to rank donor populations for which the relative magnitude of $\bar{C}_{pe\mu}$ was known. Linear regression of $\bar{C}_{pe\mu}$ on the proportion of donor germplasm accounted for 87 to 99% of the variation in $\bar{C}_{pe\mu}$ for four traits. They concluded that $\bar{C}_{pe\mu}$ precisely ranks populations or inbreds relative to frequencies of useful alleles to improve a single cross and that $\bar{C}_{pe\mu}$ should be useful in choosing parents to improve elite single crosses.

This paper presents an empirical evaluation of Dudley's (1984, 1987b) theory by applying the methods

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to populations of known composition and relationship to the single cross to be improved. Our objectives were to determine the effectiveness of $\bar{\ell}_{e\mu}'$ in identifying populations with unique dominant alleles and to determine the predictive ability of the relationship estimator.

MATERIALS AND METHODS

Genetic Materials

The seven populations used in this study were derived from a backcrossing scheme involving maize inbreds B79 and B77. The inbred B79 was selected from the Population BS10, previously designated as Iowa Two-Ear Synthetic No. 1 (Russell and Hallauer, 1976). BS10 was synthesized from 10 lines with two-eared characteristics and good combining ability (Russell et al., 1971). Inbred B77 was derived from the Population BS11, previously designated as Pioneer Two-Ear Composite (Russell and Hallauer, 1974). BS11 was synthesized by crossing southern prolific germplasm and adapted Corn Belt lines.

The single cross B79 \times B77 was backcrossed to both parents in 1982. This backcross produced two populations: one was $\approx 75\%$ B79 and 25% B77, and the other was $\approx 75\%$ B77 and 25% B79. Each of the first backcross populations was backcrossed to both parental lines in 1983, producing four populations ranging from 87.5% B79 and 12.5% B77 to 87.5% B77 and 12.5% B79. The single cross B79 \times B77 was selfed to the F_2 and became the seventh population in the study. All populations with pedigrees, population designator (P_1 to P_7), and percentage of B79 and B77 are presented in Table 1. The six backcross populations and the (B79 \times B77) F_2 population were then random-mated for two generations to approach genetic equilibrium. In each random-mating generation, 240 to 360 ears were harvested from chain-sibbed plants from each population. In the second generation of random mating, the seeds planted were from a balanced bulk of the chain-sibbed plants in the first generation.

A balanced bulk of seeds from the second random-mating generation was then testcrossed to the four maize inbreds: B79, B77, B73, and Mo17. An average of 48 plants from each population was sampled to produce the testcrosses. The minimum number of plants sampled in any population was 37. The seven populations were also testcrossed to the single crosses B73 \times Mo17 and B79 \times B77. In the testcross to the single crosses, an average of 45 plants was sampled from each population. Six single crosses were formed from the diallel cross of inbreds B79, B77, B73, and Mo17.

The genetic materials evaluated in the population cross experiment consisted of the seven populations per se, the seven populations crossed with the four inbreds, the seven populations crossed with the two single crosses, the six single crosses, and one check hybrid for a total of 56 en-

tries. In a separate experiment, the inbreds B79, B77, B73, and Mo17 per se were evaluated.

Experimental Procedures and Data Collection

The 56 entries included in the population cross experiment were evaluated in a 7 by 8 triple rectangular lattice design. The experiment was grown at the Agronomy and Agricultural Engineering Research Center near Ames, the Iowa State University Research Center near Ankeny, and at the Martinsburg, IA, test site in 1988 and 1989. The experimental units were two-row plots, 5.5 m long, with 0.76 m between rows. Plots were machine-planted at a rate of 81 330 seeds ha^{-1} and thinned at the 4- to 5-leaf stage to 62 194 plants ha^{-1} .

The four inbreds were evaluated in a randomized complete-block design with five replications. The inbred experiment was grown in the same six environments as the population cross experiment. The experimental units and plant densities for the inbred experiment were identical to those of the population cross experiment. Currently accepted management and cultural practices were used for both experiments at all locations.

Entries were evaluated for nine traits: yield of shelled grain ($mg\ ha^{-1}$) corrected to 155 $g\ kg^{-1}$ moisture, moisture concentration in shelled grain ($g\ kg^{-1}$), plant and ear heights (cm), percentage of root-lodged and stalk-lodged plants, percentage of dropped ears, and pollen and silking dates. All plots were machine harvested. Grain moisture was obtained at the time of harvest with a portable moisture tester. Plant and ear heights were calculated as the average of measurements for 10 competitive plants per plot and were measured as the distance from the ground to the node of the flag leaf (plant height) and to the highest ear-bearing node (ear height). Root lodging was calculated as the percentage of plants leaning $> 30^\circ$ from vertical. Stalk lodging was calculated as the percentage of plants broken at or below the highest ear-bearing node. Dropped ears were calculated as the percentage of ears detached from plants. Pollen and silking dates were recorded as number of days before 31 July when 50% of the plants in a plot were shedding pollen (pollen date) and 50% of the plants in a plot had emerged silks (silking date) to produce estimator values that increase with early flowering (Zanoni and Dudley, 1989). Pollen and silking date were collected only in the Ames environment in 1988 and 1989.

Statistical Analysis

Each location-year combination was treated as a random environment in both the population cross and inbred experiments. The analysis of variance for an individual environment in the population cross experiment was calculated according to the analysis for a rectangular lattice (Cochran and Cox, 1957). Means adjusted for lattice block effects were used to obtain the analysis of variance combined across environments. The genotype \times environment interaction mean square was used to test the significance of the variation due to genotypes and to calculate standard errors of all statistics reported.

The data for the individual environments in the inbred experiment were analyzed as a randomized complete-block design and then combined across environments. The genotype \times environment interaction mean square was used to test the significance of the variation due to genotypes and to calculate standard errors of all statistics reported.

Estimates of $\bar{\ell}_{e\mu}'$ were calculated for each population by using entry means averaged across all environments according to the method described by Dudley (1987b). Estimates of $\bar{\ell}_{e\mu}'$ are calculated from one of four equations (cases) chosen on the basis of the frequency of recessive alleles at loci Classes j and k in the donor population. The

Table 1. Donor populations, population designators, and the proportion of B77 and B79 within each population of maize

Population		Parents in population	
Pedigree	Designator	B79	B77
		%	
[(B79 \times B77) \times B79] \times B79	P_1	87.5	12.5
(B79 \times B77) \times B79	P_2	75.0	25.0
[(B79 \times B77) \times B77] \times B79	P_3	62.5	37.5
(B79 \times B77) F_2	P_4	50.0	50.0
[(B79 \times B77) \times B79] \times B77	P_5	37.5	62.5
(B79 \times B77) \times B77	P_6	25.0	75.0
[(B79 \times B77) \times B77] \times B77	P_7	12.5	87.5

criteria for obtaining the appropriate $\mathcal{L}\bar{p}_{e\mu}'$ case and thus determining the $\mathcal{L}\bar{p}_{e\mu}'$ estimator equation are reported in Dudley (1987b). To determine the appropriate $\mathcal{L}\bar{p}_{e\mu}'$ case, the single-cross performance must be either greater or less than the performance per se of both inbred parents. Because of the inability to determine the proper $\mathcal{L}\bar{p}_{e\mu}'$ case in all instances, estimates of $\mathcal{L}\bar{p}_{e\mu}'$ for the traits of grain moisture, stalk and root lodging, and dropped ears are not reported.

Estimates of $\mathcal{L}\bar{p}_{e\mu}'$ were calculated for yield, ear height, plant height, pollen date, and silking date. The variance of $\mathcal{L}\bar{p}_{e\mu}'$ was calculated as the variance of a linear function of means. The variance of $\mathcal{L}\bar{p}_{e\mu}'$ may be underestimated owing to errors involved in choosing the appropriate case (Zanoni and Dudley, 1989). Estimates of $\mathcal{L}\bar{p}_{e\mu}'$ were considered to be significantly different from zero when $\mathcal{L}\bar{p}_{e\mu}'$ exceeded two times the standard error of the estimate. Estimates of $\mathcal{L}\bar{p}_{e\mu}'$ within a single cross were considered to be significantly different when the difference between estimates exceed two times the standard error of the difference. The standard error of the difference is equal to the square root of the sum of variances of the $\mathcal{L}\bar{p}_{e\mu}'$ estimates in question.

The relationship estimator proposed by Dudley (1987b) was used to estimate the relationship of the populations to the parents of the single cross for grain yield. Standard errors of the relationship estimates were calculated as the square root of the variance of the linear combination of means used to calculate the estimate.

RESULTS AND DISCUSSION

Environmental conditions were poor for maize production in 1988 because of drought. Conditions in 1989 were average at the Ames and Martinsburg sites and poor at the Ankeny site because of dry conditions. The single-cross hybrids in the test averaged 6.84 and 8.17 Mg ha⁻¹ for grain yield in 1988, and 1989 and the inbreds averaged 1.86 and 3.56 Mg ha⁻¹ for grain yield in 1988 and 1989. Entry means averaged across the six environments are reported in Table 2.

There were significant ($P \leq 0.05$) treatment and treatment \times environment interaction effects for all traits in the combined analysis of variance for the population cross experiment. There were significant treatment effects for grain yield, ear height, grain moisture, stalk lodging, and plant height in the combined analysis of variance for the inbred experiment. The treatment \times environment interaction effects in the inbred experiment were significant for all traits.

Grain yield was greatest in the testcrosses of the populations to B73 and Mo17 (Table 2). Ear height was highest in testcrosses of the populations to B73. The single-cross hybrids B73 \times Mo17 and B79 \times Mo17 produced the greatest grain yields. Per se performance of the populations for grain yield and ear height displayed unexpected results (Table 2). It was expected that populations with the least inbreeding would have the greatest performance for grain yield, ear height, and plant height. The grain yield of P₇ was significantly greater than P₆, by 1.29 Mg ha⁻¹. The ear height of B77 was significantly lower than the ear height of B79 in per se performance, but ear height of P₇, which is predominantly B77, was significantly greater than P₆, P₅, and P₁.

Population P₁, which is predominantly B79, was correctly identified as having the greatest estimated number of favorable dominant alleles ($\mathcal{L}\bar{p}_{e\mu}'$) for im-

Table 2. Entry means of populations, population crosses, single crosses, and inbred lines of maize averaged across six environments.

Entry	Grain		Height		Days before 31 July	
	Yield	Moisture	Ear	Plant	Anthesis	Silking
	Mg ha ⁻¹	g kg ⁻¹	cm		d	
P ₁	3.03	229	93.7	166.8	12.4	8.7
P ₂	3.37	236	101.5	180.3	13.3	9.7
P ₃	4.09	201	98.3	185.2	18.4	14.1
P ₄	3.68	230	97.0	183.0	13.6	9.9
P ₅	2.97	222	95.1	186.8	13.9	10.2
P ₆	2.23	194	81.9	170.8	19.8	15.8
P ₇	3.52	209	102.6	198.4	18.9	15.2
P ₁ \times B77	5.33	222	110.6	204.9	16.3	13.4
P ₂ \times B77	4.25	222	108.5	203.8	15.8	12.6
P ₃ \times B77	5.61	215	108.6	205.7	17.8	14.5
P ₄ \times B77	2.87	232	97.3	194.2	13.9	10.2
P ₅ \times B77	3.36	223	97.5	193.7	14.2	10.9
P ₆ \times B77	5.70	214	108.2	215.1	20.4	16.5
P ₇ \times B77	3.65	231	102.9	208.0	15.2	11.8
P ₁ \times B79	3.25	234	99.2	173.1	12.6	9.3
P ₂ \times B79	3.73	230	98.7	176.1	13.3	10.2
P ₃ \times B79	5.02	217	109.8	180.7	16.2	13.2
P ₄ \times B79	4.38	235	106.1	189.2	14.8	12.2
P ₅ \times B79	5.21	230	109.9	194.2	15.2	12.7
P ₆ \times B79	6.22	196	110.0	196.8	20.6	17.3
P ₇ \times B79	5.36	216	113.8	192.2	17.8	14.3
P ₁ \times B73	7.54	217	123.0	209.0	17.7	14.6
P ₂ \times B73	7.32	215	117.6	209.0	18.9	15.9
P ₃ \times B73	6.89	212	114.2	207.8	20.0	16.2
P ₄ \times B73	7.13	212	117.3	211.7	18.3	15.4
P ₅ \times B73	7.33	210	117.1	213.7	18.8	15.2
P ₆ \times B73	6.99	199	110.2	209.3	21.8	18.3
P ₇ \times B73	6.92	205	114.5	214.2	19.8	16.1
P ₁ \times Mo17	7.60	197	113.9	201.6	20.1	17.7
P ₂ \times Mo17	7.11	204	115.7	205.6	20.2	16.9
P ₃ \times Mo17	7.16	194	109.2	207.0	21.1	18.2
P ₄ \times Mo17	7.01	213	107.9	201.4	19.6	16.7
P ₅ \times Mo17	7.34	218	109.5	203.4	20.0	16.5
P ₆ \times Mo17	6.25	186	100.8	206.4	21.8	18.0
P ₇ \times Mo17	6.11	206	105.8	209.5	20.9	17.3
B79 \times B77	6.51	234	117.4	210.0	18.2	14.6
B79 \times B73	7.65	219	122.2	209.1	19.0	16.1
B79 \times Mo17	8.16	201	115.6	205.9	21.0	19.0
B77 \times B73	7.49	209	116.5	220.6	18.3	14.5
B77 \times Mo17	6.59	206	102.3	202.9	20.0	16.6
B73 \times Mo17	8.64	203	113.1	215.3	20.6	17.9
SE (population experiment)	0.29	4.2	2.0	2.7	0.4	0.5
B79	2.57	241	80.1	147.6	9.8	7.6
B77	1.67	231	69.2	160.4	9.5	6.6
B73	3.33	209	84.6	168.7	11.0	9.1
Mo17	3.26	189	72.7	155.9	15.1	10.4
SE (inbred experiment)	0.23	10.7	1.8	3.9	1.5	1.0

proving the grain yield of B73 \times Mo17 (Table 3). Populations P₆ and P₇ had the smallest values of $\mathcal{L}\bar{p}_{e\mu}'$ as expected, although both values were unexpectedly smaller than the estimate of $\mu G'$ ($\mu G'$ is equivalent to $\mathcal{L}\bar{p}_{e\mu}'$, but is used for ranking inbreds rather than populations) for B77. These results agree with those of Pfarr and Lamkey (1992), who found that B79 has the largest estimated number of favorable dominant alleles for grain yield to contribute to B73 \times Mo17.

The single crosses B73 \times B77, B79 \times Mo17, B73 \times B79, and B77 \times Mo17 share one common parent with the populations. Therefore, we expect the population with the greatest percentage of the common inbred to have the smallest estimate of $\mathcal{L}\bar{p}_{e\mu}'$. For B73

Table 3. Estimates of $\mathcal{L}\bar{p}_{e\mu}'$ for the maize donor populations with six recipient single crosses for grain yield.

Inbred or population	Percentage of B79	$\mathcal{L}\bar{p}_{e\mu}'$ of single crosses to be improved					
		B73 × Mo17	B73 × B77	B79 × Mo17	B73 × B79	B77 × Mo17	B79 × B77
		Mg ha ⁻¹					
B79†	100.0	0.96*	1.12*	—	—	1.60*	—
P ₁	87.5	0.79*‡	0.93*‡	0.03	0.14	1.17*‡	-0.13
P ₂	75.0	0.63*	0.60*	0.03	0.21	0.78*	-0.28
P ₃	62.5	0.52*	0.74*	0.36*	0.42*	1.12*	0.39*
P ₄	50.0	0.56*	0.21§	0.17	0.32*	0.41*§	-0.23
P ₅	37.5	0.68*	0.38*§	0.46*	0.58*	0.61*§	0.10
P ₆	25.0	0.34*§	0.79*	0.27	0.75*	0.66*§	0.84*
P ₇	12.5	0.28§	0.35*§	0.19‡	0.51*‡	0.38*§	0.21
B77†	0.0	0.54*	—	0.44*	0.94*	—	—

* Estimate significantly different from zero at $P \leq 0.05$.

† Estimates for B79 and B77 are estimates of $\mu G'$ (Dudley, 1987a).

‡ Population expected to have the largest estimate of $\mathcal{L}\bar{p}_{e\mu}'$.

§ Estimate significantly different from population expected to have the largest estimate of $\mathcal{L}\bar{p}_{e\mu}'$.

× B77 and B77 × Mo17, P₁ was correctly identified as the population with the greatest estimated number of dominant alleles (Table 3). In these single crosses, estimates of $\mathcal{L}\bar{p}_{e\mu}'$ for P₄ through P₇ were significantly smaller than for P₁, except for P₆ when B73 × B77 was the single cross to be improved. These data suggest that B79 has unique dominant alleles not present within B73, Mo17, and B77. For B79 × Mo17 and B73 × B79, P₇ was expected to produce the greatest estimates of $\mathcal{L}\bar{p}_{e\mu}'$. Estimates of $\mathcal{L}\bar{p}_{e\mu}'$ for P₇ in both single crosses, however, were intermediate to estimates obtained for P₁ through P₆, and no significant differences were detected between P₇ and the other populations. There was generally a failure of $\mathcal{L}\bar{p}_{e\mu}'$ to identify populations with the greatest percentage of B77 when B79 was a parent of the single cross. Only two estimates of $\mathcal{L}\bar{p}_{e\mu}'$ were significantly different from zero for the single cross B79 × Mo17. All estimates of $\mathcal{L}\bar{p}_{e\mu}'$ except two were significantly different from zero for B73 × B79, although few significant differences were detected among the estimates. This may be because B77 has few unique dominant alleles for yield to contribute to the single crosses, or because estimates of $\mathcal{L}\bar{p}_{e\mu}'$ are biased by dominant alleles not contributed by B77 at other loci classes.

The single cross B79 × B77 and the populations share both parents in common. With the B79 × B77 single cross, we would expect that estimates of $\mathcal{L}\bar{p}_{e\mu}'$ for the seven populations would not be significantly different from zero and that there would be no differences among the populations for estimates of $\mathcal{L}\bar{p}_{e\mu}'$. Populations P₃ and P₆ had significant estimates of for grain yield, and the estimate of $\mathcal{L}\bar{p}_{e\mu}'$ for P₆ was significantly greater than the estimates for all other populations. These results generally agree with the expectation that the estimates of $\mathcal{L}\bar{p}_{e\mu}'$ will not be different from zero and suggest that the assumptions of complete dominance, constant genotypic value, and no epistasis are appropriate for yield.

Because higher ear height is dominant, estimates of $\mu G'$ or $\mathcal{L}\bar{p}_{e\mu}'$ detect the relative number of dominant alleles for higher ear height in the donor population for which the hybrid to be improved has recessive alleles (Zanoni and Dudley, 1989). Population P₁ had the largest estimate of $\mathcal{L}\bar{p}_{e\mu}'$ for B37 × Mo17, B73 × B77, and B77 × Mo17 (Table 4). These results are consistent with the greater frequency of dominant

alleles for ear height contributed by B79 to the single cross B73 × Mo17 (Pfarr and Lamkey, 1992). Population P₇ was also correctly identified as the population with the greatest frequency of favorable alleles for the single cross B79 × Mo17, and P₇ in the cross B73 × B79 had the second largest estimate of $\mathcal{L}\bar{p}_{e\mu}'$. There were no significant differences among the populations for the B73 × B79 single cross. All estimates of $\mathcal{L}\bar{p}_{e\mu}'$ for B79 × B77 were significantly greater than zero, indicating that $\mathcal{L}\bar{p}_{e\mu}'$ may be identifying dominant alleles at loci classes other than Class ℓ . For B79 × B77, the estimate for P₂ was significantly different from those for P₅ and P₆. Although significant estimates of $\mathcal{L}\bar{p}_{e\mu}'$ were obtained for B79 × B77, any bias in estimation of $\mathcal{L}\bar{p}_{e\mu}'$ is similar across populations because there are few significant differences among the estimates of $\mathcal{L}\bar{p}_{e\mu}'$. Estimates of $\mathcal{L}\bar{p}_{e\mu}'$ for plant height were similar to the results obtained for ear height.

Because silking date was recorded as the number of days before 31 July it is a measure of earliness. Therefore, large values of $\mathcal{L}\bar{p}_{e\mu}'$ indicate that the donor population contains dominant alleles for earliness that are not present in the single cross. Silking date produced less consistent results for ranking the populations on the basis of $\mathcal{L}\bar{p}_{e\mu}'$ estimates than did grain yield and ear height (Table 5). In the single crosses B73 × Mo17, B73 × B77, B79 × Mo17, B73 × B79, and B77 × Mo17, the population expected to produce the largest estimate of $\mathcal{L}\bar{p}_{e\mu}'$ did not, and few differences were detected among the populations. Three populations had significant estimates of $\mathcal{L}\bar{p}_{e\mu}'$ for B79 × B77. The failure of $\mathcal{L}\bar{p}_{e\mu}'$ to correctly rank the populations may be due to similar contributions of alleles from B79 and B77 for silking date, or few total loci controlling silking date. The expression of silking date may also be controlled primarily by additive gene action, and the apparent dominance may be a function of other types of gene action, such as epistasis. Estimates of $\mathcal{L}\bar{p}_{e\mu}'$ for pollen date were also calculated and were similar to the results for silking date.

The parameter $\mathcal{L}\bar{p}_{e\mu}'$ is a modification of the parameter $\mathcal{L}\bar{p}_{e\mu}$ made by removing the assumption that $\bar{p}_j = \bar{p}_k$ (Dudley, 1987b). When $\bar{p}_j \neq \bar{p}_k$, $\mathcal{L}\bar{p}_{e\mu}$ is the equal to the sum of the true value of $\mathcal{L}\bar{p}_{e\mu}$ ($\mathcal{L}\bar{p}_{e\mu}'$) and a bias term. Dudley has shown that the bias term is equal to $\{[(I_1 \times I_2) - I_1][(I_1 \times I_2) - I_2](\bar{q}_j - \bar{q}_k)\}/$

Table 4. Estimates of $\mathcal{E}\bar{p}_e\mu'$ for the maize donor populations with six recipient single crosses for ear height.

Inbred and population	Percentage of B79	$\mathcal{E}\bar{p}_e\mu'$ of single crosses to be improved					
		B73 × Mo17	B73 × B77	B79 × Mo17	B73 × B79	B77 × Mo17	B79 × B77
B79†	100.0	11.68*	10.83*	—	—	14.50*	—
P ₁	87.5	12.08*‡	11.23*‡	4.35*§	4.97*	13.20*‡	3.07*
P ₂	75.0	9.38*	8.52*	4.68*§	3.50*	13.18*	2.43*
P ₃	62.5	7.68*§	6.83*§	5.98*	5.40*	10.85*	5.52*
P ₄	50.0	9.23*	7.23*§	4.58*§	5.27*	8.43*§	3.67*
P ₅	37.5	9.13*	7.23*§	6.03*	6.17*	8.88*§	5.20*
P ₆	25.0	5.68*§	4.83*§	5.62*	3.40*	8.50*§	5.62*
P ₇	12.5	7.83*§	6.98*§	7.82*‡	5.55*‡	9.15*§	—
B77†	0.0	8.25*	—	7.85*	6.78*	—	—

* Estimate significantly different from zero at $P \leq 0.05$.
 † Estimates for B79 and B77 are estimates of $\mu G'$ (Dudley, 1987a).
 ‡ Population expected to have the largest estimate of $\mathcal{E}\bar{p}_e\mu'$.
 § Estimate significantly different from population expected to have the largest estimate of $\mathcal{E}\bar{p}_e\mu'$.

Table 5. Estimates of $\mathcal{E}\bar{p}_s\mu'$ for the maize donor populations with six recipient single crosses for silking date.

Inbred and population	Percentage of B79	$\mathcal{E}\bar{p}_s\mu'$ of single crosses to be improved					
		B73 × Mo17	B73 × B77	B79 × Mo17	B73 × B79	B77 × Mo17	B79 × B77
B79†	100.0	2.03*	2.15*	—	—	2.60*	—
P ₁	87.5	1.33*‡	1.40*‡	0.10§	0.05§	1.97*‡	0.12
P ₂	75.0	1.37*	1.85*	0.12§	0.60*§	1.57*	0.15
P ₃	62.5	1.85*	2.20*	1.20*	1.42*	2.35*	1.37*
P ₄	50.0	1.27*	1.12*	0.57	0.97*	0.92*§	0.30
P ₅	37.5	1.17*	1.25*	0.65*	1.05*	1.05*§	0.60
P ₆	25.0	2.00*	3.25*§	1.65*	2.85*§	2.25*	3.10*
P ₇	12.5	1.58*	1.70*	1.25*‡	1.67*‡	1.47*	1.22*
B77†	0.0	1.03*	—	0.95*	0.97*	—	—

* Estimate significantly different from zero at $P \leq 0.05$.
 † Estimates for B79 and B77 are estimates of $\mu G'$ (Dudley, 1987a).
 ‡ Population expected to have the largest estimate of $\mathcal{E}\bar{p}_s\mu'$.
 § Estimate significantly different from population expected to have the largest estimate of $\mathcal{E}\bar{p}_s\mu'$.

Table 6. Expected and estimated values of \bar{q}_j and \bar{q}_k for the maize donor populations with the recipient single cross B79 × B77.†

Trait	Locus class	Population						
		P ₁	P ₂	P ₃	P ₄	P ₅	P ₆	P ₇
Expected	\bar{q}_j	0.875	0.750	0.625	0.500	0.375	0.250	0.125
Expected	\bar{q}_k	0.125	0.250	0.375	0.500	0.625	0.750	0.875
Yield	$\bar{q}_j - \bar{q}_k$	(0.75)	(0.50)	(0.25)	(0.00)	(-0.25)	(-0.50)	(-0.75)
	$\bar{q}_j\bar{x}$	0.76	0.57	0.57	0.42	0.38	0.50	0.40
	$\bar{q}_k\bar{x}$	0.19	0.35	0.35	0.66	0.69	0.51	0.68
Ear Height	$\bar{q}_j\bar{x} - \bar{q}_k\bar{x}$	(0.57)	(0.22)	(0.22)	(-0.24)	(-0.31)	(-0.01)	(-0.28)
	$\bar{q}_j\bar{x}$	0.65	0.63	0.50	0.50	0.48	0.50	—‡
	$\bar{q}_k\bar{x}$	0.27	0.29	0.41	0.57	0.63	0.42	—
Silk Date	$\bar{q}_j\bar{x} - \bar{q}_k\bar{x}$	(0.38)	(0.34)	(0.09)	(-0.07)	(-0.15)	(0.08)	—
	$\bar{q}_j\bar{x}$	0.79	0.67	0.59	0.43	0.44	0.50	0.39
	$\bar{q}_k\bar{x}$	0.18	0.29	0.36	0.63	0.61	0.54	0.66
	$\bar{q}_j\bar{x} - \bar{q}_k\bar{x}$	(0.61)	(0.38)	(0.23)	(-0.20)	(-0.17)	(-0.04)	(-0.27)

† $\bar{q}_j = 1 - \bar{p}_j$ and $\bar{q}_k = 1 - \bar{p}_k$, where \bar{p}_j and \bar{p}_k are the frequency of favorable alleles at loci Classes j and k , respectively, $\bar{q}_j\bar{x}$ and $\bar{q}_k\bar{x}$ are estimates of \bar{q}_j and \bar{q}_k , respectively, from our data.
 ‡ Estimates of $\bar{q}_j\bar{x}$ or $\bar{q}_k\bar{x}$ were not calculated because \bar{q} was ≤ 0 or ≥ 1 .

$2(I_1 - I_2)$, where I_1 and I_2 are the means of the parents of the recipient single cross, $I_1 \times I_2$ is the mean of the recipient single cross, $\bar{q}_j = 1 - \bar{p}_j$, and $\bar{q}_k = 1 - \bar{p}_k$. Estimates of \bar{q}_j and \bar{q}_k are obtained by averaging upper and lower limits according to the criteria given by Dudley (1987b). Expected values of \bar{q}_j and \bar{q}_k were derived from the known pedigrees of the seven populations for B79 × B77 (Table 6). Comparison of the expected and estimated values of \bar{q}_j and \bar{q}_k reveals the accuracy of estimating upper and lower limits of \bar{q}_j and \bar{q}_k and the process of averaging to produce a mean.

Estimates of $\bar{q}_j - \bar{q}_k$ ($\bar{q}_j\bar{x} - \bar{q}_k\bar{x}$) for yield, ear height, and silking date generally agreed with the sign of the expected differences ($\bar{q}_j - \bar{q}_k$). Estimates differed from expected values in many instances, although trends were evident for most traits (Table 6). Because the percentages of B79 and B77 in each of the populations are averages, that the true values may vary about these averages, and that there are errors in evaluation and sampling of the populations, a certain amount of erroneous ranking is expected for closely related populations. Dudley (1987b) found slight differences when

comparing estimates with expected values calculated from Gerloff and Smith's (1988) hypothetical populations. Data from our study and Dudley (1987b) indicate that estimates of $\mathcal{E}\bar{p}_{\ell\mu}$ are more highly predictive of the frequency of favorable alleles at Class ℓ loci than $\mathcal{E}\bar{p}_{\ell\mu}$.

Relationship estimates of the populations to the parents of the single crosses are presented for yield (Table 7). The relationship estimator is an indicator of relative number of alleles shared between the populations and the parents of the single cross and is not a measure of consanguinity. It is therefore possible to show a relationship between a population and both parents of the single cross when examining several traits. The pedigrees of the seven populations are known, allowing comparisons of the expected and estimated relationships. All single crosses except B73 \times Mo17 have unambiguous expectations for relationships with the populations. Traditionally, the inbred B79 has combined well with C103-derived inbreds (Mo17), and the inbred B77 has combined well with BSSS-derived inbreds (B73), implying that B79 may be more similar to B73 and B77 may be more similar to Mo17 (Lee et al., 1989). The relationship of the inbreds B79 and B77 was calculated for each of the single crosses. Estimates of relationship for the inbreds were calculated by substituting the inbred (I_w) for the population (P_y) in the estimator equation (Dudley, 1987b). When the testcross performance of an inbred with itself was required, the value for the inbred evaluated per se was provided.

The relationship estimator data for grain yield indicated a relationship between B79 and B73 and between B77 and Mo17, which is in agreement with the heterotic performances of these lines. The relationship of the populations P_1 to P_5 with B73 \times Mo17, however, was not clear, and estimator values were within one standard error of zero. Lee et al. (1989) evaluated the utility of restricted fragment length polymorphisms for determining the heterotic patterns among maize inbreds. Inbreds B79 and B77 were evaluated along with three BSSS derived lines and three C103 derived lines. In a two-dimensional principal-component analysis, B77 and B79 were intermediate between the BSSS and C103 groups of inbreds, with B79 slightly closer to BSSS. The signs of the relationship estimates for the populations for B73 \times B77, B79 \times Mo17, B73 \times B79, and B77 \times Mo17 were generally as expected; the populations within a single cross usually showed a clear relationship to either B79

or B77. With the single cross B79 \times B77, populations predominantly B79 produced values indicating a relationship to B79. Similarly, populations that were predominantly B77 produced values indicating relationship to B77. These data support the predictive ability of the relationship estimators. The data from the relationship estimates suggest that the actual parameters controlling yield expression may be adequately represented by the assumptions of complete dominance, constant genotypic values, and no epistasis. The simple correlation between the relationship measures for the populations and the percentage B79 were significant for single crosses B79 \times Mo17 ($r = 0.92$), B73 \times B79 ($r = 0.86$), and B79 \times B77 ($r = 0.83$).

In summary, the relationship estimator worked well for this set of data. The parameter $\mathcal{E}\bar{p}_{\ell\mu}$ was successful in identifying populations expected to contain the largest number of dominant alleles at Class ℓ loci for grain yield and ear height. Estimates of $\mathcal{E}\bar{p}_{\ell\mu}$ were not successful in identifying populations with dominant alleles for earlier silking date. For grain yield and ear height $\mathcal{E}\bar{p}_{\ell\mu}$ was sensitive enough to distinguish only between very diverse populations (significant differences expressed between P_1 and P_6 or P_7).

A criticism of this study may be the limited sampling of the populations when testcrossed to the inbreds of the single cross (average of 48 plants sampled in each population). However, we consider that this amount of sampling was not only adequate but generous when considering the application of the method in an applied breeding program. If the breeder seeks to identify favorable exotic populations, sampling becomes even more difficult and demanding of resources.

The inability of $\mathcal{E}\bar{p}_{\ell\mu}$ to identify the expected favorable donor population when the donor populations are thought to contain a low frequency of dominant alleles at Class ℓ loci may be a concern when screening unadapted populations. In this study, populations predominately B77 failed to produce the largest estimates of $\mathcal{E}\bar{p}_{\ell\mu}$ when expected for grain yield. Exotic populations with few unique dominant alleles might possibly be masked by dominant alleles for yield already present in the single cross.

Estimates of $\mathcal{E}\bar{p}_{\ell\mu}$ cannot be calculated when the performance of the single cross is within the range of the performance of the respective inbred parents. This criterion is related to the assumption of complete dominance and restricts the application of this theory to traits displaying dominance such as grain yield, ear

Table 7. Estimates of relationships for the maize donor populations with six recipient single crosses for grain yield.

Inbreds and populations	Percentage of B79	Single cross ($I_1 \times I_2$)†					
		B73 \times Mo17	B73 \times B77	B79 \times Mo17	B73 \times B79	B77 \times Mo17	B79 \times B77
B79	100.0	0.54	-0.31	5.25*	-4.70*	0.86	4.39*
P_1	87.5	0.10	-1.38*	4.01*	-3.91*	1.48*	2.53*
P_2	75.0	-0.18	-2.24*	3.04*	-3.21*	2.07*	0.97*
P_3	62.5	0.31	-0.45	1.80*	-1.49*	0.76	1.04*
P_4	50.0	-0.09	-3.43*	2.29*	-2.37*	3.35*	-1.06*
P_5	37.5	0.05	-3.14*	1.79*	-1.74*	3.19*	-1.40*
P_6	25.0	-0.71	-0.46	-0.32	-0.39	-0.25	-0.07
P_7	12.5	-0.78	-2.44*	0.41	-1.18*	1.67*	-1.26*
B77	0.0	-0.87	-4.99*	-0.26	-0.60	4.12*	-4.39*

* Estimate of relationship significantly different from zero at $P \leq 0.05$.

† Positive values indicate that the population is more closely related to I_1 and negative values indicate a closer relationship with I_2 .

and plant height, and flowering dates. Of the nine traits measured, only grain yield, ear height, and plant height produced meaningful estimates of $\mathcal{L}\bar{p}_{e\mu}'$.

Our study differs from Hogan and Dudley's (1991) study primarily in the genetic structure of the donor populations. Hogan and Dudley (1991) created donor arrays by crossing a line or population with the recipient single cross (FRB73 \times FRMo17) in ways that produced populations that ranged from 0% donor population (the recipient single cross) to 100% donor germplasm (the donor line or population) in 25% increments. With this crossing scheme, they expected a linear relationship between $\mathcal{L}\bar{p}_{e\mu}'$ and the proportion of donor germplasm, because \bar{p}_e (the frequency of favorable alleles at Class ℓ loci) changed proportionately across the donor array. They reported that linear regression accounted for 87 to 99% of the variation in $\mathcal{L}\bar{p}_{e\mu}'$ for four traits. They concluded that $\mathcal{L}\bar{p}_{e\mu}'$ precisely ranks lines relative to the frequency of alleles at Class ℓ loci and should be useful in selecting parents to improve single crosses.

We expected a linear relationship between $\mathcal{L}\bar{p}_{e\mu}'$ and the percentage of B79 in the donor populations only for the four recipient single-crosses that shared a common parent with the donor populations and B73 \times Mo17, assuming the donor populations had favorable alleles to contribute to these single crosses. We evaluated the effectiveness of $\mathcal{L}\bar{p}_{e\mu}'$, however, on the basis of whether the estimates were significantly different from zero and whether estimates for specific donor populations were significantly different from the donor expected to have the largest estimate of $\mathcal{L}\bar{p}_{e\mu}'$. We chose this approach because, when the method is applied to donor populations of unknown merit, the best donor will be chosen on the basis of whether the estimate of $\mathcal{L}\bar{p}_{e\mu}'$ is significant and significantly different from the other donor populations. Therefore, our conclusions about the effectiveness of $\mathcal{L}\bar{p}_{e\mu}'$ in ranking and identifying populations, particularly when the frequency of dominant alleles at Class ℓ is low, differ from the conclusions of Hogan and Dudley (1991).

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