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An alternative statistic for identifying lines useful for improving parents of an elite single cross *

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Summary. Theory and methods for identifying inbred lines (I_w) with favorable dominant alleles not present in an elite single cross ($I_1 \times I_2$) have been developed recently. Selected I_w lines can be crossed to I_1 or to I_2 to transfer new favorable alleles to the single cross. However, favorable alleles already present in the single cross may be lost during selection. It is important to consider both potential gain of favorable alleles from I_w and loss of favorable alleles already present in $I_1 \times I_2$. The "net improvement" statistic (NI) = maximum $[(I_1 \times I_w - I_1 \times I_2)/2, (I_2 \times I_w - I_1 \times I_2)/2]$ estimates the number of loci where favorable alleles can be gained minus the number of loci where favorable alleles can be lost in the single cross. Because $I_1 \times I_2$ is constant in an experiment, the method reduces to choosing I_w lines with the best mean performance in combination with either I_1 or I_2. NI was compared to estimators previously proposed for identifying lines, namely: (1) minimally biased estimates ($\mu G'$) of favorable dominant alleles present in I_w but not in I_1 and I_2; (2) minimum estimate of an upper bound (UBND) on μG; and (3) predicted three-way cross (PTC) performance. Based on a set of maize (*Zea mays* L.) grain yield data, correlations among the four estimators were relatively high, but indicated that rankings of I_w lines vary with the particular estimator used. Rankings of three I_w lines based on the frequency of F_2 test crosses superior to B73 × Mo17 were identical to rankings based on NI, but differed from rankings based on $\mu G'$, PTC, and UBND. NI also was the best predictor of the mean of the upper 10% ($\bar{x}_{0.1}$) of $(I_2 \times I_w)$ $F_2 \times I_1$ or $(I_1 \times I_w)$ $F_2 \times I_2$ test crosses based on simulated data. Being a simple statistic highly correlated to $\bar{x}_{0.1}$, NI may be useful in applied breeding programs.

Key words: Pedigree breeding – Favorable alleles – Parent selection – Single cross – *Zea mays* L.

Introduction

In many commercial maize (*Zea mays* L.) breeding programs, inbred lines are developed from base populations formed by crossing one of the parents (e.g., I_1) of an elite single cross ($I_1 \times I_2$) to another inbred (I_w). Selfing in the $(I_1 \times I_w)$ F_2 or BC_1 population and test crossing to I_2 are done to isolate a new inbred which, when crossed to I_2, will produce a hybrid superior to $I_1 \times I_2$. The choice of donor inbred lines (I_w) is crucial to the success of such breeding programs. Dudley (1984, 1987) developed theory and methods for identifying inbred lines with the largest number of favorable dominant alleles not present in either parent of the single cross. The statistic $\mu G'$ estimates the relative number of new favorable alleles in I_w.

Single cross performance is improved if favorable alleles are transferred from I_w to either I_1 or I_2 during selection. However, this occurs only at the risk of losing favorable alleles already present in the elite single cross. Net improvement in hybrid performance results only if the number of favorable alleles gained in the single cross is greater than the number of favorable alleles lost during selection.

The objective of this paper is to present and evaluate a statistic that considers both potential gain of favorable alleles from I_w and loss of favorable alleles already present in $I_1 \times I_2$ in identifying lines useful for improving the parents of an elite single cross.

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Theory

Assume + and − are the favorable and less favorable alleles, respectively, affecting a quantitative trait. Eight classes of loci exist for any three homozygous lines (Dudley 1984) (Table 1). Let A, B, C, D, E, F, G, and H be the number of loci in their respective classes. The genotypic values of the three possible genotypes (+ +, + −, − −) at a single locus are $z+2\mu$, $z+\mu+a\mu$, and z, respectively, where μ is half the difference between homozygote values and a is the degree of dominance. Assume complete dominance ($a=1$), negligible epistasis, and that z, μ and a are constant for N total loci. The genotypic values for each line and for all possible crosses among the three lines can be expressed in terms of the above genetic parameters (Table 2). Dudley (1987) developed equations for estimating the relative number of B, C, D, E, F, and G loci while confounding $\mu\,(A-H)$ with $N\,(z+\mu)$. If the three inbred lines are the parents of a single cross (I_1 and I_2) and a third inbred (I_w), potential improvement in hybrid performance exists at class G loci, which are − − in I_1 and I_2 but + + in I_w. Hence, Dudley (1987) proposed choosing I_w lines with large estimates of $\mu G'$, a minimally biased estimate of the relative number of class G loci.

It is assumed that the elite single cross has the best performance for the trait of interest. Thus, the mean of $I_1 \times I_2$ is greater than or equal to that of either $I_1 \times I_w$ or $I_2 \times I_w$. Otherwise, hybrid performance for the trait of interest can be improved simply by substituting I_w for either I_1 or I_2 in the single cross and either $I_1 \times I_w$ or $I_2 \times I_w$ would be the new single cross to be improved. $I_1 \times I_2 - I_1 \times I_w$ and $I_1 \times I_2 - I_2 \times I_w$ estimate $2\mu\,(F-G)$ and $2\mu\,(D-G)$, respectively. Therefore, both F and D will be greater than or equal to G.

If I_2 is the parent crossed to I_w, + alleles can be gained at class G but lost at class F loci. With complete dominance, no change in single cross performance is expected at classes B, C, D, and E because I_1 is + + at B, C, and D loci, while I_2 and I_w are + + at class E loci. With equal locus effects, a gain of one + allele at a class G locus will be offset by a loss of one + allele at a class F locus.

Let P be the probability of fixing a + allele. The following relationships exist: Prob (fix at least one + allele at class G) $=1-$Prob (all − − at class G)$=1-(1-P)^G$; and Prob (lose at least one + allele at class F)$=1-$Prob (all + + at class F)$=1-P^F$. Thus, the chance of fixing + alleles at class G loci increases, while that of losing + alleles at class F loci decreases as P approaches 1. If $P=1$, the probability of losing + alleles at class F loci is zero, and only class G loci determine improvement in the single cross. With selection, $P=1/(2-s)$, where s is the selection coefficient against the recessive homozygote (Johnson 1980). $s=i_\alpha\,2\mu/\sigma$ (Falconer 1982), where i_α is the selection differential with α% of the individuals selected, $2\mu/\sigma$ is the standardized locus effect, and σ is the phenotypic standard deviation of the trait. Comstock (1974) suggested $2\mu/\sigma$ values ranging from 0.05 to 0.125. With a proportion of 1% selected and $2\mu/\sigma=0.125$, P is equal to 0.6. Thus, even with strong selection pressure and large locus effects, values of P are probably closer to 0.5 (value of P in the absence of selection) than to 1, so that both classes F and G loci determine net improvement in hybrid performance.

The chance of gaining + alleles at class G loci increases as G increases, while the chance of losing + alleles at class F loci decreases as F decreases. Therefore, a logical approach is to select I_w lines with large $\mu\,(G-F)$ values. Because $F \geq G$, $\mu\,(G-F)$ has a maximum value of zero, and maximum net improvement in the single cross will occur if $F=G$. This result is consistent with previous findings, indicating that the probability of isolating a new line superior to either parent is maximum if the favorable alleles are equally distributed between the two parents (Johnson 1980; Dudley 1982). The statistic $\mu\,(G-F)$ was proposed by Dudley (1984) to determine whether to self directly in the F_2 or to backcross to I_2 or I_w prior to selection. However, Dudley outlined a two-step process of calculating (1) $\mu G'$ and (2) $\mu\,(G-F)$ so that the lines with highest $\mu G'$ values do not necessarily have the highest $\mu\,(G-F)$ values. Also, $\mu\,(G-F)$ estimates the difference between expected means of the $I_1 \times (I_2 \times I_w)$ F_2 test cross population and $I_1 \times I_2$ (Zanoni and Dudley 1989a).

Table 1. Genotypes at classes of loci possible for the inbred parents (I_1 and I_2) of a single cross and a third inbred (I_w) (from Dudley 1984)

Class of loci	I_1	I_2	I_w
A	+ +	+ +	+ +
B	+ +	+ +	− −
C	+ +	− −	+ +
D	+ +	− −	− −
E	− −	+ +	+ +
F	− −	+ +	− −
G	− −	− −	+ +
H	− −	− −	− −

Table 2. Genotypic values of I_1, I_2, I_w, and the crosses among them under a general gentic model[a] (from Dudley 1987)

$$I_1 = N\,(z+\mu)+\mu\,(A+B+C+D-E-F-G-H)$$
$$I_2 = N\,(z+\mu)+\mu\,(A+B-C-D+E+F-G-H)$$
$$I_w = N\,(z+\mu)+\mu\,(A-B+C-D+E-F+G-H)$$
$$I_1 \times I_2 = N\,(z+\mu)+\mu\,(A+B+C\,a+D\,a+E\,a+F\,a-G-H)$$
$$I_1 \times I_w = N\,(z+\mu)+\mu\,(A+B\,a+C+D\,a+E\,a-F+G\,a-H)$$
$$I_2 \times I_w = N\,(z+\mu)+\mu\,(A+B\,a+C\,a-D+E+F\,a+G\,a-H)$$

[a] N=total number of loci; z=value of the − − genotype; μ=half the difference between homozygote values; a=degree of dominance; A, B, …, H=number of loci in their respective classes

If I_1 is the parent crossed to I_w, + alleles can be gained at class G but + alleles can be lost at class D loci. The appropriate statistic is then $\mu\,(G-D)$. Therefore, a statistic that measures potential net improvement in hybrid performance is defined as NI$=$maximum$[\mu\,(G-F),\ \mu\,(G-D)]=\mu G-$minimum$(\mu F,\ \mu D)$. $\mu\,(G-F)$ is calculated as $(I_1 \times I_w - I_1 \times I_2)/2$, while $\mu\,(G-D)$ is calculated as $(I_2 \times I_w - I_1 \times I_2)/2$. Because $I_1 \times I_2$ is constant, the method reduces to choosing I_w lines with the best mean performance in combination with either I_1 or I_2. If $I_1 \times I_w > I_2 \times I_w$, then I_w is crossed to I_2 and I_1 is used as the tester. Otherwise, I_w is crossed to I_1 with I_2 as the tester.

Compared to $\mu G'$, NI is a simpler statistic but has a relatively larger standard error. The estimators of $\mu G'$ proposed by Dudley (1987) are slightly biased if the numbers of certain classes of loci are unequal. NI is free from this bias. While $\mu G'$ estimates potential improvement in single cross performance, which is likely to be achieved only with long-term selection, NI is probably a better predictor of intermediate and short-term gains.

One must be careful in interpreting results if I_w is closely related to either I_1 or I_2. For the extreme case of I_2 and I_w being genetically identical, the number of classes F and G loci are zero, and $I_1 \times I_2$ and $I_1 \times I_w$ are expected to have the same mean. Consequently, NI is equal to the maximum theoretical value of zero but no improvement (nor any loss) in single cross performance can be expected. To have genetic diversity between I_w and

I_1 or I_2, knowledge of pedigree relationships or genetic background would be useful in conjunction with NI.

NI can be calculated if $I_1 \times I_2$ does not have the highest mean performance for the trait of interest. If $I_1 \times I_w$ or $I_2 \times I_w \geq I_1 \times I_2$, then $G \geq D$ or F so values of NI will be positive. A backcross to I_w will be useful if NI is significantly greater than zero to increase the probability of isolating a new superior line (Dudley 1982, 1984).

For a crop wherein production of large amounts of F_1 seed is difficult, F_2 and inbred data can be used to calculate NI. $\mu(G-F) = (I_1 \times I_w)\,F_2 - (I_1 \times I_2)\,F_2 + (I_2 - I_w)/4$ and $\mu(G-D) = (I_2 \times I_w)\,F_2 - (I_1 \times I_2)\,F_2 + (I_1 - I_w)/4$.

Computer simulation study

Computer simulation was used to study the correlation of a superiority measure with NI, $\mu G'$, the predicted three-way cross (PTC) performance (Sprague and Eberhart 1977), and minimum upper bound (UBND) on μG (Gerloff and Smith 1988). PTC is calculated as $(I_1 \times I_w + I_2 \times I_w)/2$ and has the expectation $I_w(I_1 \times I_2) = N(z+\mu) + \mu(A+B+C+E+G-H)$. UBND is the minimum of $I_1 \times I_w - I_1$ and $I_2 \times I_w - I_2$ and has the expectation $\mu\,[2G + \text{minimum}\,(2E, 2C)]$.

The superiority measure considered was the mean of the upper 10% of test crosses ($\bar{x}_{0.1}$) of random inbred lines from the F_2 of $I_1 \times I_w$ (or $I_2 \times I_w$) to I_2 (or I_1). $\bar{x}_{0.1} = \bar{x} + i_{0.1}\,\sigma_G\,h$, where $\bar{x}$ = overall mean of test crosses, $i_{0.1}$ = standardized selection differential (1.755 for 10% selected), σ_G = test cross genetic standard deviation, and h = square root of heritability. If I_1 is the tester and I_2 is crossed to I_w, $\bar{x} = N(z+\mu) + \mu\,[A + (B+C)(1+a)/2 + (D+E)\,a + (F+G)(a-1)/2 - H]$ and $\sigma_G = \mu\,[(B+C)(1-a)^2 + (F+G)(1+a)^2]^{0.5}/2$. With complete dominance, $\bar{x} = N(z+\mu) + \mu(A+B+C+D+E-H)$ and $\sigma_G = \mu(F+G)^{0.5}$. If I_2 is the tester and I_1 is crossed to I_w, $\bar{x} = N(z+\mu) + \mu\,[A + (B+E)(1+a)/2 + (C+F)\,a + (D+G)(a-1)/2 - H]$ and $\sigma_G = \mu\,[(B+E)(1-a)^2 + (D+G)(1+a)^2]^{0.5}/2$. With complete dominance, $\bar{x} = N(z+\mu) + \mu(A+B+C+E+F-H)$ and $\sigma_G = \mu(D+G)^{0.5}$.

A hypothetical trait controlled by 200 unlinked, nonepistatic loci with equal effects was considered. Dominance was either partial ($a = 0.5$) or complete and $-z = \mu = 1$. The quantities $(A+B) = i$, $(C+D) = j$, $(E+F) = k$, and $(G+H) = l$ are constant for a given single cross. A single cross with $i = j = k = l = 50$ (Single Cross 1) and another with $i = 40$, $j = 75$, $k = 50$, and $l = 35$ (Single Cross 2) were considered. The latter corresponds to a single cross with three class j for every two class k loci, such as B73 (I_1) × Mo17 (I_2) (Zanoni and Dudley 1989 a). Twohundred I_w lines with uniformly random numbers of classes A, B, C, D, E, F, G, and H loci (subject to the above restrictions on numbers of classes i, j, k, and l loci and $G \leq D$ or F) were simulated. Means of I_1, I_2, I_w, $I_1 \times I_2$, $I_1 \times I_w$, and $I_2 \times I_w$ were determined based on their genetic expectations. Random normal deviates representing nongenetic effects were added to the genotype means to give phenotypic means. The random normal deviates were scaled such that means are zero and median $h^2 = 0.25$ or 0.5. The case of $h^2 = 1$ was also considered. Because the appropriate $\bar{x}$ and σ_G for calculating $\bar{x}_{0.1}$ depends on whether I_w is crossed to I_1 or to I_2, the quantity $(\mu C + \mu F - \mu D - \mu E) = I_2 \times I_w - I_1 \times I_w - (I_2 - I_1)/2$ was calculated (Dudley 1984). I_w is crossed to I_1 if the above quantity is positive and to I_2 if negative.

$\bar{x}_{0.1}$ was more highly correlated with NI than with either $\mu G'$, PTC, or UBND in 9 out of the 12 cases (combinations of single cross, heritability levels, and levels of dominance) considered (Table 3). All correlation coefficients between $\bar{x}_{0.1}$ and each of the four estimators were significantly greater than zero with average values of 0.84, 0.79, 0.80, and 0.67 for NI, $\mu G'$, PTC, and UBND, respectively. If $h^2 = 1$, the average (over single crosses and levels of dominance) correlations of $\bar{x}_{0.1}$ with NI, $\mu G'$, PTC, and UBND were 0.95, 0.85, 0.86, and 0.75, respectively. Thus, NI is expected to be superior to either $\mu G'$, PTC, and UBND in the ideal situation of nongenetic variance equal to zero. The superiority of NI over the other estimators decreased as h^2 decreased to 0.5 or 0.25. With lower heritabilities, the correlation of NI with $\bar{x}_{0.1}$ was as large or slightly larger than those for $\mu G'$, PTC, or UBND.

Table 3. Correlation coefficients of NI, $\mu G'$, PTC, and UBND with the mean of the upper 10% ($\bar{x}_{0.1}$) of test crosses based on simulated data

Degree of dominance (a)	h^2	Single cross	Correlation[a] with $\bar{x}_{0.1}$:			
			NI	$\mu G'$	PTC	UBND
1.0	1.0	1	0.95	0.86	0.90	0.68
1.0	1.0	2	0.95	0.75	0.75	0.58
1.0	0.5	1	0.80	0.79	0.83	0.62
1.0	0.5	2	0.77	0.69	0.66	0.44
1.0	0.25	1	0.77	0.72	0.75	0.45
1.0	0.25	2	0.62	0.59	0.58	0.35
0.5	1.0	1	0.97	0.95	0.97	0.87
0.5	1.0	2	0.92	0.85	0.80	0.88
0.5	0.5	1	0.84	0.85	0.91	0.84
0.5	0.5	2	0.85	0.80	0.81	0.82
0.5	0.25	1	0.79	0.80	0.89	0.75
0.5	0.25	2	0.79	0.78	0.76	0.75
Average correlations:						
$a = 1.0$			0.81	0.73	0.75	0.52
$a = 0.5$			0.86	0.84	0.86	0.82
	$h^2 = 1.0$		0.95	0.85	0.86	0.75
	$h^2 = 0.5$		0.82	0.78	0.80	0.68
	$h^2 = 0.25$		0.74	0.72	0.74	0.58
		SC = 1	0.85	0.83	0.88	0.70
		SC = 2	0.82	0.74	0.73	0.64
Overall correlation			0.84	0.79	0.80	0.67

[a] All correlation coefficients are significantly greater than zero ($P = 0.05$)

Table 4. Grain yield means[a] (Mg ha^{-1} dry wt) of ^{w} lines when crossed to B84 (^{1}) and to Mo17 (^{2}) and estimates of $\mu\,(G-F)$, $\mu\,(G-D)$, and NI

I_w	$I_w\times$B84	$I_w\times$Mo17	$\mu\,(G-F)$[b]	$\mu\,(G-D)$	NI	Cross I_w to:
Pa91	11.05	8.71	−0.2	−1.4	−0.2	Mo17
B73	7.91	10.41	−1.8	−0.5	−0.5	B84
Va26	10.11	8.48	−0.7	−1.5	−0.7	Mo17
H100	8.85	9.93	−1.3	−0.8	−0.8	B84
B75	9.60	8.07	−0.9	−1.7	−0.9	Mo17
B77	9.36	9.53	−1.0	−1.0	−1.0	B84
B79	9.35	8.94	−1.0	−1.2	−1.0	Mo17
H95	9.30	8.32	−1.1	−1.6	−1.1	Mo17
N152	9.20	9.11	−1.1	−1.2	−1.1	Mo17
H102	9.07	6.44	−1.2	−2.5	−1.2	Mo17
N7A	8.04	8.92	−1.7	−1.3	−1.3	B84
B57	8.80	7.71	−1.3	−1.9	−1.3	Mo17

[a] From Zanoni and Dudley (1989a). LSD (0.05) for hybrid means = 1.01. Mean of B84 × Mo17 = 11.42

[b] Values of $\mu(G-F)$ or $\mu(G-D)$ less than -0.5 are significantly ($P=0.05$) different from zero. LSD (0.05) for $\mu(G-F)$ or $\mu\,(G-D)=0.7$

Table 5. Correlation coefficients[a] among NI, $\mu G'$, PTC, and UBND when B84 × Mo17 (above diagonal) and N152 × Mo17 (below diagonal, are the single crosses to be improved

	NI	$\mu G'$	PTC	UBND
NI		0.83*	0.75*	0.42^{NS}
$\mu G'$	0.96*		0.84*	0.85*
PTC	0.92*	0.98*		0.66*
UBND	0.86*	0.97*	0.97*	

^{NS}, * Nonsignificant and significant at $P=0.05$, respectively

[a] Calculated from data of Zanoni and Dudley (1989a) and Mišević (1989a)

The distribution of favorable alleles between the two parents of the single cross affected the correlation of $\bar{x}_{0.1}$ with the estimators. For all four estimators, correlations with $\bar{x}_{0.1}$ were higher for Single Cross 1, which had equal numbers of loci that are + + in both I_1 and I_2 (class *i*), + + in I_1 but − − in I_2 (class *j*), − − in I_1 but + + in I_2 (class *k*), and − − in both I_1 and I_2 (class *l*). The decrease in correlation with $\bar{x}_{0.1}$ due to unequal numbers of classes *i*, *j*, *k*, and *l* loci (Single Cross 2) was largest for PTC and smallest for NI. Although limited to a sample of two single crosses, this result suggests that NI is least affected by variation in the distribution of favorable alleles between the two parents of the single cross.

Compared to $\mu G'$, PTC or UBND, the NI statistic was more highly correlated with $\bar{x}_{0.1}$ regardless of level of dominance. Although complete dominance was assumed in the derivation of all four estimators, correlations with $\bar{x}_{0.1}$ were higher if dominance was partial ($a=0.5$) rather than complete. With arbitrary dominance, the expectations of the estimators are: NI = maximum $\{[(G-F)(a+1)+(C-B)(1-a)]\mu/2,\ [(G-D)(a+1)+(E-B)(1-a)]\,\mu/2\}$; $PTC=N\,(z+\mu)+\mu\,[A+a\,(B+G)+(C+E)\,(a+1)/2-(D+F)\,(1-a)/2-H]$; and UBND = minimum $\{\mu\,[(G+E)\cdot(a+1)-(B+D)(1-a)],\ \mu\,[(G+C)(a+1)-(B+F)(1-a)]\}$. The expectation of $\mu G'$ with arbitrary dominance depends on which of four equations are used to estimate the parameter (Dudley 1987). For example, the expectation of $\mu G'$ is $\mu\,[2\,G\,(a+1)-2\,B\,(1-a)+(C-D)\,(a+1)+(E-F)\,(1-a)]/4$ for the case $\bar{q}_{j0}$, $\bar{q}_{j1}$.

If dominance is partial, the + + homozygote has a greater genotypic value than the heterozygote, and maximum performance is achieved if both parents of the single cross carry the + allele. If I_1 is the tester and I_2 is crossed to I_w, gain of + alleles occurs at classes *C* and *G* while loss of + alleles occurs at classes *B* and *F*. If I_2 is the tester and I_1 is crossed to I_w, gain of + alleles occurs at classes *E* and *G* while loss of + alleles occurs at classes *B* and *D*. Except for the positive contribution of *B* to PTC with arbitrary dominance, classes wherein gain of + alleles is possible (*C*, *E*, and *G*) have a positive contribution, while classes wherein loss of + alleles is possible (*B*, *D*, and *F*) have a negative contribution to the expectations of all four estimators considered. Because the expectations of the estimators reflect changes in the classes of loci which determine net gain of + alleles as the degree of dominance decreases, these methods are still useful for identifying donor inbred lines even with partial dominance.

Illustration and application

Grain yield data from a 14-parent diallel experiment (Zanoni and Dudley 1989a) are used to illustrate the method. The 14 maize inbreds were public lines of Stiff Stalk Synthetic (B73, B84, N7A, and H100), Lancaster (Pa91, H102, H95, Va26, and Mo17), and unrelated (B77, B79, B75, B57, and N152) origin. The diallel crosses were evaluated at two locations near Urbana/IL in 1984 and

Table 6. Estimates of NI, $\mu G'$, PTC, and UBND and frequency of test crosses superior to B73 × Mo17 for grain yield (Mg ha^{-1}) (data from Mišević 1989 b)

Population	NI	$\mu G'$	PTC	UBND	Superior testcrosses:[a]	
					TC_H	TC_{LSD}
B73 × (N152 × Mo17) F_2	0.45	2.75	13.3	9.17	36	4
B73 × (Pa91 × Mo17) F_2	0.25	1.21	10.1	4.35	21	2
B73 × (Va26 × Mo17) F_2	−0.78	1.29	10.5	6.72	11	0

[a] TC_H = number of test crosses with yield higher than check yield; TC_{LSD} = number of test crosses with yield higher than the check yield by at least one LSD. Fifty test crosses from each population were evaluated

1985. Being the highest-yielding cross, B84 (I_1) × Mo17 (I_2) was designated the single cross to be improved.

Pa91 had the largest (i.e., closest to zero) values for NI among the potential donor inbred lines (Table 4) followed by B73. For Pa91, $\mu(G-F)=(11.05-11.42)/2=-0.19$, while $\mu(G-D)=(8.71-11.42)/2=-1.36$. NI = minimum $[\mu(G-F), \mu(G-D)]=-0.19$. Because $I_1 \times I_w$ (11.05) is greater than $I_2 \times I_w$ (8.71), Pa91 should be crossed to Mo17 (I_2). Because Mo17 and Pa91 are lines of Lancaster origin, the Stiff Stalk × Lancaster heterotic pattern of the elite single cross is maintained. The heterotic pattern is also maintained for the other I_w lines as well.

Except for the correlation between NI and UBND, correlation coefficients among NI, $\mu G'$, PTC, and UBND were significantly greater than zero if B84 × Mo17 is the hybrid to be improved (Table 5). General combining ability effect of I_w (Zanoni and Dudley 1989 a) is also highly correlated to NI ($r=0.80^*$). Correlation coefficients among the estimators were higher using the data of Mišević (1989 a) with N152 × Mo17 as the single cross to be improved. Regardless of the target single cross, the correlation with NI was largest for $\mu G'$ and smallest for UBND. This result was also obtained from simulated data, wherein correlations with NI were 0.86^*, 0.83^*, and 0.66^* for $\mu G'$, PTC, and UBND, respectively. The correlation coefficients, particularly for B84 × Mo17, indicate that rankings of I_w lines for improving a single cross vary with the estimator of favorable alleles used. Although Pa91 had the highest estimates of $\mu G'$, PTC, UBND (Zanoni and Dudley 1989 a), and NI, these statistics ranked the other I_w lines differently.

For the F_2 test cross data of Zanoni and Dudley (1989 b), the rankings of I_w lines based on either NI, $\mu G'$, PTC, or UBND did not correlate with rankings based on actual test cross performance. For the data of Mišević (1989 b), NI was superior to the other statistics in predicting the frequency of superior test crosses. Based on the number of test crosses better than the check (B73 × Mo17), N152 is the best line, Pa91 is intermediate, and Va26 is the poorest line for improving the single cross (Table 6). While the rankings of N152, Pa91, and Va26 based on NI and frequency of superior test crosses were identical, Va26 was ranked higher than Pa91 based on $\mu G'$, PTC, or UBND.

Estimation of NI requires similar testing resources as $\mu G'$, UBND, and PTC. With n I_w lines, estimation of all four statistics requires evaluating n $I_1 \times I_w$ and n $I_2 \times I_w$ hybrids in a sufficient number of environments. In addition, $I_1 \times I_2$ is evaluated to estimate NI and $\mu G'$, while I_1 and I_2 are evaluated to estimate $\mu G'$ and UBND. If three-way cross, i.e., $I_w (I_1 \times I_2)$, data are used instead of PTC, half the amount of testing resources are needed compared to NI.

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