Evaluation of three test statistics used to identify maize inbred lines with new favorable alleles not present in elite single cross *

D. Miševič

Maize Research Institute "Zemun Polje", S. Bajica 1, P.O. Box 89, 11081 Zemun, Yugoslavia

Summary. The identification of inbred lines useful for improvement of an elite single cross hybrid is an essential part of a pedigree maize (*Zea mays* L.) breeding program. The objectives of this study were to identify lines that could be useful for improvement of hybrid B73 × Mo17 and to relate the values of estimators of new favorable alleles with test cross yields. Crosses of parents of hybrid B73 × Mo17 with 10 public lines from the United States (US), and 14 Maize Research Institute "Zemun Polje" proprietary lines (lines per se, and test crosses from 3 F_2 populations) were evaluated at 4 locations in Yugoslavia in 1986. Significant differences in grain yield were found among lines in minimally biased estimates of favorable alleles (μG) present in a donor inbred but not present in a B73 × Mo17, in minimum upper bound (UBND) estimates and in predicted three-way performance (PTC). Twenty-one lines had a significant number of dominant favorable alleles for grain yield not present in B73 × Mo17. The highest values for all estimators of new favorable alleles were found for donor lines which belonged to different heterotic groups than the B73 and Mo17. For most of the inbreds, the $(C+F)-(D+E)$ statistics agreed with predigree information. Simultaneous increases in grain yield and decreases in grain moisture content for B73 × Mo17 are possible with several donor inbred lines. All of the lines with a high number of new favorable alleles for grain yield not present in B73 × Mo17 had negative μD (F) $-\mu G$ values for low plant height. Line N152 had the most new favorable alleles for grain yield not present in single cross B73 × Mo17. Population (N152 × Mo17) F_2 had the highest difference of observed test cross means from check mean, the most test crosses with significantly higher yields than the check, and the largest estimate of number of segregating loci.

Introduction

Elite maize (*Zea mays* L.) inbreds are a useful source of favorable alleles for improving a superior single cross. Recent developments in quantitative genetic theory (Dudley 1984a, 1984b; Gerloff 1985) provide methods for identifying inbred lines that could be used in improving parents of elite single crosses.

Zanoni and Dudley (in preparation) evaluated a diallel set of 14 inbred lines – which included 4 Stiff Stalk Synthetic (SSS), 5 Lancaster Sure Crop, and 5 Corn Belt dent lines unrelated to SSS and Lancaster – and estimated the relative number of favorable alleles for grain yield for each of the lines relative to selected target hybrids. Miševič (in preparation) used a 15-line diallel which included 3 SSS, 2 Lancaster Sure Crop, 3 US Corn Belt dent lines unrelated to SSS and Lancaster Sure Crop and 7 lines originated from Yugoslavian open-pollinated varieties; I also estimated the relative number of favorable alleles for each of the lines relative to seven target hybrids representing different heterotic patterns. The ability of proposed estimators in discriminating among donor lines was reported.

Zanoni and Dudley (in preparation) evaluated test crosses from six F_2 populations from maize inbreds

selected for favorable alleles not present in an elite single cross. They found that F_2 test cross populations developed from inbred lines with large estimates of favorable alleles had, on the average, more test crosses genetically superior to the check mean than those from inbreds with low estimates.

A large number of adapted inbred lines of maize are available for improvement of elite single crosses. Breeders are interested in how to identify inbreds with favorable alleles not present in a target single cross. In this experiment, we studied a genetically broad sample of inbred lines adapted to the Yugoslavian Corn Belt. Selected inbreds represented at least four heterotic groups (Mišević, in preparation). Our objectives were to identify inbred lines for the improvement of the hybrid B73 × Mo17 and to obtain additional information on the relationship between estimators of new favorable alleles and test cross performance.

Materials and methods

Two experiments were conducted. In experiment 1, crosses of 24 inbreds with both parents of the hybrid B73 × Mo17 were made. Inbreds were selected to represent major heterotic groups from the United States (US) and Yugoslavia (YU) (Table 1). Only elite US public and proprietary Maize Research Institute "Zemun Polje" lines were used. In experiment 2, the yields of individual test crosses from three F_2 populations were measured.

Crosses of donor lines with B73 and Mo17 were made at the Maize Research Institute nursery at Zemun Polje in 1985. Forty-eight hybrids and target hybrid B73 × Mo17 were grown together with a 15-line diallel (number of hybrids were common to both experiments) (Mišević, in preparation) in 1986 in a 12 × 12 triple lattice design at four locations in Yugoslavia. At each location, an inbred trial was grown adjacent to the hybrid trial. For the inbred evaluation, a randomized complete block design (RCB) with five replications was used. Twenty-four lines were grown. Single row plots were used in hybrid and inbred trials. Each plot consisted of 20 plants spaced 26 cm and 23 cm in the hybrid and inbred trial, respectively. The distance between rows was 70 cm in both trials. Plot sizes were 3.64 m^2 in the hybrid and 3.22 m^2 in the inbred trial. Population density was 54,900 and 62,100 plants ha^{-1} in the hybrid and inbred tirals, respectively. Planting and harvesting were done by hand at each location. All plots were overplanted and thinned to desired stands.

Analysis of variance was performed for grain yield (adjusted to 140 g kg^{-1} moisture and expressed in kg ha^{-1}), grain moisture (g kg^{-1}) and plant height (cm) in each location. For each individual analysis, there was no gain in efficiency for the lattice design relative to a randomized complete block design. Therefore, a randomized complete block analysis was used for each trait in the combined analysis of variance over four locations. Replications and locations were considered random and genotypes were considered fixed effects.

Criteria for improvement were: increased grain yield, reduced grain moisture and reduced pant height. Increase in yield is the primary goal of most of the maize breeding programs. On the other hand, identification of inbreds with favorable alleles for low moisture in grain and/or lower plant height, as well as high grain yield not present in B73 × Mo17, would be highly desirable. Hybrid B73 × Mo17 was selected as the target hybrid. This hybrid consists of two public inbreds. It was widely grown

Table 1. Inbreds and their parentage

Line	Source
	USA SSS lines
B73	BSSS (R) C5
B84	BS13 (S2) CO
N7A	Oh7 × SSS
	USA Lancaster related lines
Mo17	C103 × 187-2
Pa91	(Wf9 × Oh40B) S$_4$ × (38 − 11 × L317) 38 − 11 − S$_4$
	USA Other lines
N152	Nebr. B IV syn.
B77	BS11
B79	BS10
H102	Mayrobela × C123
Va26	Oh43 × K155
	YU lines
V395	Vukovar Yellow Dent
V158	Vukovar Yellow Dent
R455	Ruma Yellow Dent
R59	Ruma Yellow Dent
R70z	Ruma Yellow Dent
S144	Sid Yellow Dent
L105	Italian Long-ear Flint
P37-2	Italian Long-ear Flint
T768	Timok Yellow Flint
Do37-2	Yellow Dent from Dolovo
	Lancaster related and YU related lines
70/9	C103 × NS796
HC439	Hybrid Arizona 439* × C103
LTC68	C103 selection for prolifacy**
	Other lines
LD230	Prolific A × R588 × Calqueno

* Mexican June × YU varieties
** C103 × Ladyfinger

in the US and Europe and represents the predominant heterotic pattern for a large part of the temperate region.

Minimally biased estimates of favorable alleles present in the donor inbred, but lacking in the hybrid (μG), were calculated using the modified procedure given by Dudley (1987). For any three homozygous lines, eight classes of loci (A, ..., H) exist, as shown in Table 2 and described by Dudley (1984a). Let A, ..., H be the number of loci in each class as well as designation of the class. The genotypes + +, + −, and − − were assigned genotypic values of μ, a μ, and −μ, respectively, where μ is half the difference between + + and − − genotypes. Assuming complete dominance (a = 1), A = H, z = −μ, and no epistasis, genotypic values for each line and each possible F$_1$ among the three lines can be written in terms of B, C, D, E, F, G, and μ (Dudley 1984a). Solving equations for μB, μC, ... μG the original estimate was:

$$\mu G = [(I_1 \times I_w) + (I_2 \times I_w) - (I_1 \times I_2) - I_1 - I_2 - I_w]/4$$

In the modified procedure free of assumptions that A = H and z = −μ (Dudley 1987), the estimate of μG was obtained by using the appropriate one of the following expressions:

$$\mu G = [(I_1 \times I_w) + (I_2 \times I_w) - (I_1 \times I_2) - I_1]/4 \qquad \text{if } \bar{q}_{jo}, \bar{q}_{k1};$$

$$\mu G = [(I_1 \times I_w) + (I_2 \times I_w) - (I_1 \times I_2) - I_2]/4 \qquad \text{if } \bar{q}_{j1}, \bar{q}_{ko};$$

$$\mu G = [2(I_2 \times I_w) - (I_1 \times I_2) - I_2]/4 \qquad \text{if } \bar{q}_{jo}, \bar{q}_{j1};$$

$$\mu G = [2(I_1 \times I_w) - (I_1 \times I_2) - I_1]/4 \qquad \text{if } \bar{q}_{ko}, \bar{q}_{k1}.$$

Table 2. Genetic status of classes of loci possible for three homozygous lines

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

* + loci homozygous for favorable alleles; − loci homozygous for unfavorable allele

In these expressions, $\bar{q}_{j0}$, $\bar{q}_{j1}$, $\bar{q}_{k0}$, and $\bar{q}_{k1}$ represent the use of $\bar{q}_j = 0$ or $\bar{q}_k = 0$ to estimate minimum values of $\bar{q}_j$ and $\bar{q}_k$ from the expression $I_1 \times I_w - I_2 \times I_2 = (I_1 \times I_2 - I_2) q_j - (I_1 \times I_2 - I_1) q_k$. If the expression is solvable for $q_j = 0$, (i.e. $0 < q_k < 1$ when $q_j = 0$) then $\bar{q}_{j0}$ is used to estimate minimum values for q_j and q_k. Similarly $\bar{q}_{j1}$ and $\bar{q}_{k1}$ represent acceptable solutions if $\bar{q}_j = 1$ or $\bar{q}_k = 1$. The expressions q_j and q_k represent frequencies of recessive alleles at the class j and k loci, respectively. Class j (C + D in Table 2) loci are + + in I_1 and − − in I_2 while class k (E + F in Table 2) loci are − − in I_1 and + + in I_w. Thus q_j and q_k are equivalent to D/(C + D) and E/(E + F), respectively.

Other statistics used were minimum upper bound (UBND) estimates (Gerloff 1985) and predicted three-way cross (PTC) means (Sprague and Eberhart 1977). The UBND is defined as the minimum of two expressions $(I_1 \times I_w) - I_1$ and $(I_2 \times I_w) - I_2$ which have expectations of $2\mu E + 2\mu G$ and $2\mu C + 2\mu G$, respectively. The predicted three-way cross was computed as $[(I_1 \times I_w) + (I_2 \times I_w)]/2$ and had expectation of $N(z+\mu) + \mu(A + B + C + E + G - H)$ (Zanoni and Dudley, in preparation) where N is the total number of loci affecting a trait.

The method also allows estimation of the relative relationship of I_w lines to I_1 and I_2. As defined by Zanoni and Dudley (1986), (C + F) − (D + E) = $[2(I_1 \times I_2) - 2(I_1 \times I_w) - I_2 + I_1]/2$. Significant positive and negative (C + F) − (D + E) estimates indicate that I_w is more closely related to I_1 and I_2, respectively. This statistics do not necessarily imply consanguinity, although on average consanguineous pairs of lines will generally show less heterosis than nonconsanguineous pairs.

For deciding whether to start selfing directly in F_2 generation or whether at least one backcross to either the parental or donor inbreds is advisable, $\mu G - \mu D$ or $\mu G - \mu F$ statistics were used.

Error variances were calculated using the usual expression for the variance of the linear function for μG, PTC, UBND, (C + F) − (D + E) and $\mu G - \mu D$, or $\mu G - \mu F$. For μG and $\mu G - \mu D$ the resulting standard error may be an underestimate (Zanoni and Dudley, in preparation). Least significant difference values were calculated by multiplying the standard error of the difference by two.

To find the relationship between estimators of new favorable alleles and the actual yield of test crosses, three donor lines (N152, Va26 and Pa91) were selected for improvement of B73 × Mo17. Lines N152, Va26 and Pa91 were found to have highest estimates of μG within the group of US public lines evaluated in other experiments at Zemun Polje and Urbana in 1984 (J. W. Dudley, personal communication). Mo17 was the parent to be improved by all donor lines because it was more closely related to each of three lines. Selfing was initiated within F_2 populations. To find the relationship between test cross performance and estimates of new favorable alleles, 50 plants from each population were selfed and simultaneously crossed to B73 in 1985. Fifty test crosses from each population were grown in separate but adjacent experiments at two locations in Yugoslavia in 1986. The test crosses were evaluated in randomized complete block design with three replications. The check hybrid, B73 × Mo17, was entered three times in each block. One-row plots were used with plot size and population densities identical to the hybrid trial in experiment 1.

Genotypic differences among test crosses were tested for significance using an F-test with the genotype by environment interaction as the error term. To estimate genetic components, the estimated mean squares were equated to expected values and solved for the desired variance component. A 90% confidence interval was calculated (Williams 1962). Variance components from different populations were considered different from each other when their confidence intervals did not overlap.

Heritability estimates (h^2) on a testcross mean basis were calculated as the ratio of genetic variance (σ_g^2) to phenotypic variance (σ_p^2). A 90% confidence interval for h^2 was calculated according to Knapp et al. (1985). Estimates were considered to be different from zero when the confidence interval did not include zero. The relative number of loci (n) in classes B, D, E and G (Dudley 1984a) segregating in each F_2, and the predicted difference of test cross means from check mean $(\mu_{TC} - \mu_c)$ were calculated for each F_2 using equations $n = \mu B + \mu D + \mu E + \mu G = (I_1 \times I_w) - (I_1 + I_w)$ and $\mu_{TC} - \mu_c = \mu G - \mu D$ (assuming complete dominance) (Zanoni and Dudley, in preparation).

The means of all test crosses from a population were calculated. In addition, each test cross mean was expressed as a deviation from the check mean. A 95% confidence interval was calculated for each deviation using the t-distribution (Steel and Torrie 1980). Deviations were considered to be different from zero when their confidence intervals did not include zero.

Interpretation of results

Numerous studies, including this one, show directional dominance of favorable alleles for grain yield. Positive μG values for grain yield indicate the presence of new favorable alleles. Significant negative values for $\mu G - \mu D$ or $\mu G - \mu F$ suggest that at least one backcross to I_1 or I_2 should be made before inbreeding. If $\mu G - \mu D$ or $\mu G - \mu F$ values are not significantly different from zero, direct selfing from the F_2 is suggested. Negative values for $\mu G - \mu D$ or $\mu G - \mu F$ indicate that the number of loci for which I_1 or I_2 carry favorable and I_w unfavorable alleles is larger than the number of loci for which I_1 or I_2 carry unfavorable and I_w favorable alleles, and backcrossing to I_1 or I_2 is suggested. On the other hand, if $\mu G - \mu D$ or $\mu G - \mu F$ is positive, the number of loci for which I_1 or I_2 carry unfavorable and I_w favorable alleles is larger than the number of loci for which I_1 or I_2 carry favorable and I_w unfavorable alleles. Backcrossing to I_w is suggested (Dudley 1984b). When I_w is more closely

related to I_1 and I_2, respectively, $\mu G - \mu D$ and $\mu G - \mu F$ should be used.

Because grain yield was the trait for which heterotic patterns are most important, relationship values for moisture content and plant height were not calculated. Decisions of either backcrossing or selfing from the F_2 were also made based on the grain yield parameters.

Alleles for high grain moisture and high plant height are dominant, therefore favorable alleles for low moisture and low plant height are recessive (Table 4). In this case, the objective is to add recessive favorable alleles which can be expressed in the hybrid. If I_1 is to be improved, then class D loci (Dudley 1984a) are important because I_w contains recessive alleles and I_2 is homozygous recessive (Table 2). Thus, high values of μD are desirable. In this case unfavorable dominants will be present in I_w at class G loci. The difference $\mu D - \mu G$ is a measure of the value of I_w if I_1 is to be improved and $\mu F - \mu G$ when I_2 is to be improved. If these values are > 0, then the probability is at least 0.5 that a new experimental F_2 derived line will have more loci homozygous recessive for favorable alleles than the line being improved, assuming μ constant for all loci.

Results and discussion

Grain yield

Highly significant differences $(P < 0.01)$ in grain yield among hybrids and among inbreds were found in the combined analysis of variance. Genotype × environment interaction was also highly significant in both trials. Hybrid means calculated over four locations ranged from 6,217 to 14,262 kg ha^{-1}, while inbred means ranged from 1,975 to 5,648 kg ha^{-1} (Table 4). Significant differences $(P < 0.05)$ were found between B73 and Mo17 single crosses. B73 single crosses were on the average 936 kg ha^{-1} higher in yield than Mo17 single crosses (Table 3). Significant parent × lines interaction was detected for grain yield. Significant differences were also found among lines in μG, TC and UBND values. Values of $(C + F) - (D + E)$ and $\mu G - \mu D$ or $\mu G - \mu F$ were significantly different from zero for most of the inbreds (Table 5).

Twenty-one of 22 inbreds had positive μG values for grain yield. The line H102 was the only inbred with negative μG value (Table 5). This line was released as a genetic stock for specific disease resistance, rather than as a parental line with superior combining ability. The highest-ranked line for μG and UBND was N152. Yugoslavian and YU-related lines were ranked from second to 14th place for μG and 13th for UBND (Table 5). Lines T768 and Do37-2 were ranked higher

Table 3. Means of lines × B73, lines × Mo17 and B73 × Mo17

Entries	Grain yield (kg ha^{-1})	Grain moisture (g kg^{-1})	Plant height (cm)
Lines **			
× B73	11,809*	244*	308
× Mo17	10,873	225	303
B73 × Mo17	12,745	250	301

* Differences between lines × B73 and lines × Mo17 significant at 0.05 level using F-test
** Means of 23 single crosses

than other YU lines. Neither line has any SSS or Lancaster Sure Crop germplasm (Table 1). Third-ranked for μG was LTC68. This line is related to Lancaster Sure Crop in that it carries C103 germplasm. Stiff Stalk Synthetic and Lancaster Sure Crop lines were ranked low.

Line T768 was ranked first by PTC and second by UBND, and Do37-2 was ranked third by all three estimators of new favorable alleles not present in hybrid B73 × Mo17. Good agreement was found among μG, PTC and UBND for the three highest-ranked inbreds, N152, T768 and Do37-2. Line LTC68, however, ranked 3 d, 6th and 8th by μG, UBND and PTC, respectively. For the group of donor lines, the correlations among estimators of new favorable alleles was positive and highly significant. The coefficient of correlation between μG and PTC, μG and UBND and PTC and UBND was 0.96, 0.91 and 0.92, respectively. Similar correlations among the same estimators were reported by Mišević (in preparation) for different target hybrids.

The relationship of donor lines to Mo17 and B73 agrees with pedigree information. Stiff Stalk Synthetic lines (B84, N7A) were related to B73. Lancaster Sure Crop (Pa91) and Lancaster Sure Crop-related lines (70/9, LTC68, HC439) were related to Mo17. US Corn Belt dent lines which do not belong to SSS and Lancaster Sure Crop groups were unrelated to either parent, with the exception of B79. This line was found to be more closely related to B73. Half of the YU lines were unrelated to either parent of the B73 × Mo17, four were related to Mo17 and three were related to B73. Pedigrees of T768 and P3-72 did not indicate a relationship to either parent of the target hybrid, but T768 was more closely related to B73 and P3-72 to Mo17.

The most useful lines for improvement of single-cross hybrid B73 × Mo17 seem to be N152, T768, LTC68 and Do37-2. These lines had high, positive and significant μG values, indicating the presence of new favorable alleles lacking in B73 × Mo17. All lines had $\mu G - \mu D$ (F) values not significantly different from zero, indicating that the number of loci for which B73 or Mo17 had unfavorable

Table 4. Grain yield, grain moisture and plant height of lines and single crosses

Line	Grain yield (kg ha^{-1})			Grain moisture (g kg^{-1})			Plant height (cm)		
	Per se	B73	Mo17	Per se	B73	Mo17	Per se	B73	Mo17
B73	4,468	–	12,745	250	–	251	221	–	301
Mo17	2,604	12,745	–	154	251	–	210	301	–
B84	5,648	8,500	14,262	250	270	254	218	275	310
N7A	4,507	10,935	11,133	231	284	241	190	288	293
Pa91	2,618	13,236	6,956	242	295	230	187	314	261
Va26	2,737	11,187	9,832	189	232	203	192	313	293
N152	4,654	13,641	13,000	202	280	239	212	310	313
B77	3.870	8,911	8,864	206	226	203	221	288	291
B79	2,434	11,117	6,447	252	264	204	202	295	278
H102	1,975	6,217	6,611	239	241	230	222	283	274
L105	2,086	12,573	12,214	180	245	210	213	314	311
V158	5,219	11,930	12,615	182	222	211	231	314	319
R70z	2,648	10,671	10,731	164	201	201	204	311	314
V395	5,208	12,845	12,153	212	186	222	221	311	312
70/9	4,916	12,356	8,665	196	225	232	219	318	299
S144	4,153	11,946	12,757	190	240	252	198	297	304
R59	3,378	10,857	10,904	174	209	198	203	300	302
LTC68	5,701	13,392	11,013	212	262	239	237	322	314
LD230	4,738	13,694	11,254	190	240	210	227	315	314
HC439	4,104	13,358	9,494	210	245	223	239	324	317
P3-72	4,223	12,987	11,137	161	241	216	199	321	303
T768	–	13,196	13,350	–	278	285	–	337	321
Do37-2	–	13.029	12,350	–	242	215	–	318	323
R455	4,172	12,303	11,594	161	230	214	221	310	299
LSD 0.05	692	1,321	1,321	16	15	15	11	10	10

and donor lines favorable alleles is not different from the number of loci for which B73 or Mo17 had favorable and donor lines unfavorable alleles. In this case, backcrossing to either parent or donor line would not increase the frequency of favorable alleles in source population, and direct selfing from F_2 is recommended. New favorable alleles from N152 and Do37-2 should be incorporated in hybrid B73 × Mo17 by crossing it to either parent because both donor lines were unrelated to B73 and Mo17. T768 had positive and significant $(C+F)-(D+E)$ estimate. In this case, established heterotic pattern should be most properly used by incorporation of new favorable alleles from T768 in the more related line B73. In constrat, line LTC68 had negative and significant $(C+F)-(D+E)$ estimate and was more closely related to Mo17. Crossing to Mo17 was suggested.

In agreement with the results of Dudley (1987), Zanoni and Dudley (in preparation), and Misevic (in preparation), the results of this experiment also indicated that, within this divergent group of lines, the estimators used were able to detect differences among donor inbreds in the relative number of loci with new favorable alleles for grain yield not present in B73 × Mo17. The highest values for all three estimators of new favorable alleles were found for donor lines which belonged to a different heterotic pattern than parents of a hybrid designated to

be improved. US Corn Belt dent lines unrelated to SSS and Lancaster (N152) and a large number of YU lines were found to have the highest number of new favorable loci for grain yield not present in B73 × Mo17. Among YU and YU-related lines, the highest values of all three estimators of new favorable alleles were found for lines not directly related to US Corn Belt dent germplasm, or for lines which carry some proportion of exotic germplasm (V. Trifunović, personal communication).

Grain moisture

Significant differences in grain moisture among hybrids and among inbreds were detected in the combined analysis of variance. Mean grain moisture of single crosses was 234 g kg^{-1}. This was less than the mean grain moisture of target hybrid B73 × Mo17 (Table 4). B73 single crosses were 19 g kg^{-1} higher in grain moisture than Mo17 single crosses (Table 3).

Seventeen lines had positive $\mu D (F) - \mu G$ values, indicating the presence of favorable alleles for low grain moisture not present in B73 × Mo17 (Table 5). The largest positive values of $\mu D (F) - \mu G$ were found for B77, R70z and R59. However, these lines were ranked low by all three estimators of new favorable alleles for grain yield. For simultaneous improvement in grain yield

Table 5. Estimates of relative number of loci for grain yield when B73 × Mo17 is $I_1 \times I_2$

| Line | Case | Grain yield | | | | | Grain moisture | Plant height |
		(C+F)−(D+E)	μG−μD(F)	μG	PTC	UBND	μD(F)−μG	μD(F)−μG
B84	$j_0 k_1$	6,692*	756*	1,387 (14)	11,381 (13)	4,032[1] (20)	−1.5	−4.5
N7A	$j_0 k_1$	1,128*	−808*	1,214 (16)	11,034 (14)	6,467[1] (14)	5.0	4.0
Pa91	$j_1 k_0$	−5,348*	246	1,211 (17)	10,096 (19)	4,352[2] (19)	−22.0	−6.5
Va26	$k_0 k_1$	−424	−779*	1,290 (15)	10,505 (18)	6,719[1] (13)	9.5	−6.0
N152	$k_0 k_1$	291	127	2,751 (1)	13,320 (2)	9,173[1] (1)	6.0	−6.0
B77	$k_0 k_1$	885*	−1,940*	152 (21)	8,887 (20)	4,443[1] (18)	24.0	6.5
B79	$j_1 k_0$	−3,738*	−814*	554 (20)	8,782 (21)	3,843[2] (21)	−6.5	11.5
H102	$k_0 k_1$	1,326*	−3,067*	−729 (22)	6,414 (22)	1,749[1] (22)	10.5	9.0
L105	$k_0 k_1$	−573	−265	1,983 (8)	12,393 (6)	8,105[1] (8)	3.0	−5.0
V158	$j_0 k_1$	1,617*	−65	1,833 (11)	12,272 (7)	7,462[1] (10)	20.0	−7.0
R70z	$j_0 k_1$	992*	−1,007*	1,047 (19)	10,701 (16)	6,203[1] (16)	25.0	−6.5
V395	$k_0 k_1$	240	−296	2,119 (7)	12,499 (4)	8,377[1] (7)	14.0	−5.5
70/9	$j_1 k_0$	−2,760*	−194	1,418 (13)	10,510 (17)	6,061[2] (17)	13.0	−8.5
S144	$j_0 k_1$	2,193*	6	1,760 (12)	12,126 (9)	7,028[1] (11)	−0.5	−1.5
R59	$j_0 k_1$	979*	−920*	1,141 (18)	10,880 (15)	6,407[1] (15)	26.5	−0.5
LTC68	$j_1 k_0$	−1,447*	324	2,264 (3)	12,202 (8)	8,409[2] (6)	6.0	−10.5
LD230	$j_1 k_0$	−1,508*	474	1,876 (9)	12,474 (5)	8,650[2] (4)	5.5	−7.0
HC439	$j_1 k_0$	−2,932*	306	2,194 (5)	11,426 (12)	6,890[2] (12)	3.0	−11.5
P3-72	$k_0 k_1$	−918*	121	2,190 (6)	12,062 (10)	8,519[1] (5)	5.0	−10.0
T768	$j_0 k_1$	1,624*	571	2,467 (2)	13,542 (1)	8,728[1] (2)	−17.0	−10.0
Do37-2	$k_0 k_1$	253	−197	2,211 (4)	12,689 (3)	8,651[1] (3)	18.0	−12.0
R455	$k_0 k_1$	223	−575	1,848 (10)	11,948 (11)	7,835[1] (9)	18.5	1.0

LSD 0.05 μG for comparison $j_0 k_1$ vs. $k_0 k_1$ and $j_1 k_0$ vs. $j_0 j_1$ = 476, for other comparisons LSD 0.05 = 508; LSD 0.05 TC = 953; LSD 0.05 UBND (UBND$_1$ vs. UBND$_1$ or UBND$_2$ vs. UBND$_2$) = 1,347, (UBND$_1$ vs. UBND$_2$) = 1,526

Table 6. Grain yield (kg ha^{-1}) of test crosses from three different F_2 populations using B73 as a tester

Population	σ_g^2	n	$\bar{x}_{TC}-\bar{x}_C$	$\mu_{TC}-\mu_C$	h^2	TC_a	TC_b	TC_c
B73 × (Va26 × Mo17) F_2	251.2**	4,491**	−514	−779**	0.38	11	0	6
B73 × (N152 × Mo17) F_2	391.1**	5,742**	544	127	0.49*	36	4	1
B73 × (Pa91 × Mo17) F_2	404.0**	1,734**	163	246	0.58*	21	2	3

* Significantly different from zero at the 10% probability level
** Larger than 2 × SE
σ_g^2 = genetic variance among test crosses; n = number of segregating loci = μB+μD+μE+μG or μB+μC+μF+μG; $\bar{x}_{TC}-\bar{x}_C$ = observed difference between test cross population and check mean; $\mu_{TC}-\mu_C$ = expected difference between test cross population and check mean (μG−μD or μG−μF); h^2 = heritability; TC_a = number of test crosses with yield higher than check yield; TC_b = number of test crosses with yield for at least one LSD value higher than check yield; TC_c = number of test crosses with yield for at least one LSD value lower than the check yield

and grain moisture of B73 × Mo17, lines Do37-2, V158 and V395 should be used. These three lines were ranked high by all three estimators of new favorable alleles for grain yield and had large positive μD (F)−μG values for grain moisture. The first-ranked line in μG for grain yield (N152) also had a positive μD (F)−μG value for grain moisture, although it was approximately three times lower than for lines Do37-2, V158 and V395.

Plant height

Target hybrid B73 × Mo17 had lower plant height than most of the hybrids evaluated (Table 4). There were no significant differences between B73 and Mo17 single crosses in plant height (Table 3). Only four lines had positive μD (F)−μG values indicating the presence of a larger number of favorable alleles for lower plant height in classes D or F loci than unfavorable dominant at class G. However, all of these lines had low μG values for grain yield. Line R455 was the highest-ranked line in μG for grain yield which had a positive μD (F)−μG value for plant height. It was ranked tenth in μG for grain yield. The line with highest positive μD (F)−μG value for lower plant height (B79) was ranked 21st in μG for grain yield.

Simultaneous improvement in grain yield and plant height of B73 × Mo17 with this set of donor lines would not be as successful as the improvement of each trait alone. If both criteria are important, advantage should be given to one of these two traits.

Test crosses

Highly significant differences ($P<0.01$) were found among test crosses from each of the three F_2 populations. Checks versus test crosses also had significant mean squares for each population. F_2 populations Pa91 × Mo17 and N152 × Mo17 had a positive and Va26 × Mo17 and a negative difference of the predicted test cross means from the check mean. Only the Va26 × Mo17 difference was significant. None of the observed differences of the test cross means from the check mean was significant, although the difference for B73 × (N152 × Mo17) F_2 was positive and for B73 × (Va26 × Mo17) F_2 negative (Table 6). F_2 populations N152 × Mo17, Pa91 × Mo17 and Va26 × Mo17 had 36, 21 and 11 test crosses higher than the check mean, respectively. Four out of 50 (N152 × Mo17) F_2 test crosses were one LSD value higher in yield than target hybrid B73 × Mo17, while one was significantly lower (Table 6). Within the (Pa91 × Mo17) F_2 population, two test crosses were significantly higher and three significantly lower in yield than B73 × Mo17. Population (Va26 × Mo17) F_2 did not have any test crosses significantly better than, but had six test crosses significantly lower in yield than B73 × Mo17.

The number of loci segregating in the F_2 generation was significantly different from zero for all three populations indicating variation among test crosses (Table 6). Significant genetic variability was found in each population. The genetic variances were not significantly different from each other. F_2 populations N152 × Mo17 and Pa91 × Mo17 had, respectively, the largest and lowest estimate of the number of loci segregating (Table 6). Heritability for grain yield was intermediate for all populations, although (Pa91 × Mo17) F_2 had the highest estimate.

These preliminary results agreed with values for estimators of new favorable alleles (Table 5). Line N152 was identified as one with the most favorable alleles for improvement of hybrid B73 × Mo17. Relative to the other two populations, (N152 × Mo17) F_2 had a higher (although not significant) observed difference of test cross means from the check mean, more test crosses with a significantly higher yield and fewer test crosses with significantly lower yield than target hybrid B73 × Mo17. Disagreement between estimated µG values and test cross yield was found when Va26 was used as a donor parent of favorable alleles. Although positive µG values were found for Va26, none of the test crosses from Va26 × Mo17 population significantly exceeded the yield of B73 × Mo17. Backcrossing to Mo17 before selfing would probably improve the performance of Va26 × Mo17 test crosses, as was indicated by µG − µD value.

References

Dudley JW (1984a) A method of identifying lines for use in improving parents of a single cross. Crop Sci 24:355–357

Dudley JW (1984b) Identifying parents for use in a pedigree breeding program. In: Loden HD, Wilkinson D (eds) Proc 39th Annu Corn and Sorghum Ind. Res Conf. Am Seed Trade Assoc, Washington/DC, pp 176–188

Dudley JW (1987) Modification of methods for identifying inbred lines useful for improving parents of elite single crosses. Crop Sci 27:944–947

Gerloff JE (1985) Choice of method for identifying germplasm with superior alleles. PhD Diss, Iowa State University, Ames

Knapp SJ, Stroup WW, Ross WM (1985) Exact confidence intervals for heritability on a progeny mean basis. Crop Sci 25:192–194

Sprague GF, Eberhart SA (1977) Corn breeding. In: Sprague E (ed) Corn and corn improvement, 2nd ed. Am Soc Agron, Madison/WI, pp 305–363

Steel RG, Torrie JH (1980) Principles and procedures of statistics. McGraw-Hill, New York

Williams JS (1962) A confidence interval for variance components. Biometrics 49:278–281

Zanoni U, Dudley JW (1986) Identification of useful inbred lines for improvement of elite hybrids. Proc 22nd Annu Ill Corn Breeders School. University of Illinois, Urbana