Evaluation of Populations for Their Potential to Improve Three Maize Hybrids

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ABSTRACT

Identification of sources of favorable alleles to improve existing hybrids is one of the most important problems facing a maize (*Zea mays* L.) breeder. Previous work has demonstrated the effectiveness of a procedure developed by Dudley for identifying populations containing favorable alleles not present in an elite hybrid. However, previously reported work involved at most two elite hybrids. The objective of this study was to evaluate the potential of 20 improved populations to improve the three hybrids made from three inbreds in commercial use. Each of the populations was crossed to LH195, LH212, and LH216. The population × inbred crosses, the three hybrids among the inbreds, and the three inbreds were evaluated in seven U.S. midwestern environments in 1993 and four in 1994. Traits measured were grain yield, grain moisture, plant height, ear height, and concentration of protein, oil, and starch in the grain. For grain yield, 15 of the 20 populations had significant estimates of dominant favorable alleles not present in the highest yielding target hybrid (LH195 × LH212). None of the populations showed potential for reducing ear height. However, seven populations had more favorable recessive alleles than unfavorable dominants for plant height when LH195 × LH212 was the target hybrid. None of the populations tested appeared to have potential for increasing starch concentration in any of the target hybrids. Eight populations showed potential for increasing protein concentration in all three target hybrids. Assumptions required to identify parents were not met for grain moisture, oil concentration, and stalk and root lodging.

THE IDENTIFICATION of parental germplasm is one of the most important questions facing a plant breeder. In maize breeding, this question can be posed as how to identify populations that have alleles that will improve existing hybrids (Dudley, 1984a,c). Procedures have been developed for identifying populations or inbreds that contain favorable dominant alleles not present in a hybrid (Dudley, 1984a,b,c, 1987a,b; Metz, 1994; Bernardo, 1990a,b) and for determining the parent to which a particular population or inbred was more closely related (Dudley, 1984c). In addition, methods for identifying recessive favorable alleles are available (Dudley, 1988a) as are methods for determining whether it would be more advantageous to backcross before initiating a selfing program (Dudley, 1988b). A number of studies have evaluated inbreds and populations for their potential for improving a single cross hybrid (Dudley, 1988b; Hogan and Dudley, 1991; Pfarr and Lamkey, 1992a,b; Zanoni and Dudley, 1989a,b,c). Stojšin and Kannenberg (1995) used two target hybrids, but no study evaluating three target hybrids has been published. The objective of this study was to evaluate 20 improved populations for their potential to improve three possible hybrids.

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MATERIALS AND METHODS

The genetic materials included 20 maize populations and three commercial inbreds (Table 1). The inbreds, LH195, LH212, and LH216, were provided by Holden's Foundation Seeds (Williamsburg, IA). Each population was crossed to each inbred using at least 100 plants of the population as the female parent. A balanced bulk of seed was made for each population × inbred cross by taking equal quantities of seed from each ear in the cross. At the same time, the three possible crosses among the inbreds were made.

The 60 population × inbred crosses, the three crosses among the inbreds, and two commercial checks were grown in a generalized lattice design with 13 blocks of five entries and three replications in 11 environments. The environments included four locations in Iowa (Ames, Ankeny, Crawfordsville, and Martinsburg), two locations near Urbana, IL, and one location near Whiteland, IN, (provided by Holden's Foundation Seeds) in 1993. In 1994, the experiments were grown near Ames and Fairfield, IA, and two locations near Urbana, IL. The three inbreds were grown in randomized block designs with 10 replications in the same fields and adjacent to the population × inbred cross experiments. In all environments, plots consisted of two rows 0.76 m apart. Row length was 5.33 m in Illinois, 5.49 m in Iowa, and 6.13 m in Indiana. Standard production practices were used at all locations. Planting dates for each environment are shown in Table 2.

Grain yield (tons per hectare adjusted to 155 g kg^{-1} moisture), grain moisture, stalk lodging, and root lodging were measured in all environments. Plant and ear height were measured in all environments except Ames 1993 and Whiteland 1993. Flowering date (days from planting to mid-silk) was measured in five environments. Protein, starch, and oil concentrations in grain were measured using a Dickey-John (Auburn, IL) GACIII near-infrared analyzer (Dudley and Lambert, 1992). Data were obtained from the four Illinois environments.

Each of the 11 location × year combinations was considered a separate environment in the analysis of variance. For each environment, the population × inbred cross experiment was analyzed as a generalized lattice design using the INCANOV program by Carmer and Kratzke (1988). Adjusted means were then used for a combined analysis across environments. To test for significance of the genotype × environment interaction, the intra-block mean squares pooled across environments were used as an error term. Environments were considered random. For the inbred experiments, a combined analysis of variance across all environments was obtained using PC SAS (SAS Institute, 1993).

The procedures described by Dudley (1987a, 1988a) were used to estimate $l\bar{p}_l\mu$, $j\bar{q}_j\mu$, $k\bar{q}_k\mu$, and relationship values. The variables j, k, and l represent the number of loci in classes j, k, and l, respectively. Class j loci have dominant alleles in inbred Parent 1 (I_1) that are not present in inbred Parent 2 (I_2); class k loci have dominant alleles in I_2 that are not present in I_1; and class l loci have dominant alleles in population Y (P_y) that are not present in I_1 or I_2. The value $\bar{p}_l$ is the average frequency of dominant alleles in P_y at class l loci while $\bar{q}_j$ and $\bar{q}_k$ are average frequencies of recessive alleles in P_y at class j and class k loci, respectively. The value μ is half the difference between homozygotes at a locus and is assumed to be constant across all loci. Thus, $l\bar{p}_l\mu$ measures the relative number of

Table 1. Description of maize populations and inbreds included in the evaluation study.

Population or inbred	Description
B84R(H15)C1	Cycle 1 of half-sib selection for root pulling strength in B84R. B84R resulted from crossing B84, as a female to BSSS, planting the F_1 in an isolated field, with B84 as a male, detasseling the F_1, selecting 10% of the F_1 plants based on root pulling and recombining (L.L. Darrah, 1992, personal communication).
RBS10(C6)	Cycle 6 of reciprocal selection using an inbred tester in an Illinois high-yield environment beginning with BS10 (FR)C4 as C0 (Lambert, 1989).
BS11(FR)C10	Cycle 10 of full-sib reciprocal selection for grain yield of BS11 (Pioneer two-ear composite) (Hallauer et al., 1974).
BS16(CB)C4	Cycle 4 of S_1-progeny selection for resistance to first and second generations of the European corn borer (*Ostrinia nubilalis* Hübner) beginning with BS16(S2)C2 as the C0. BS16 was an Eto Composite adapted to the midwestern USA (Russell and Guthrie, 1991).
BS17(CB)C4	Cycle 4 of S_1-progeny selection for resistance to first and second generations of the European corn borer in BS17. Population is related to Stiff Stalk Synthetic (Russell and Guthrie, 1991).
BS26	A synthetic composed of primarily Lancaster Surecrop germplasm (Hallauer, 1986).
BS27	Cycle 6 of mass selection for adaptation to temperate environments in the Antigua composite (Hallauer, 1992).
BS28	Cycle 5 of mass selection for adaptation to temperate environments in a composite of Tuxpeño germplasm (Hallauer, 1994).
BS29	Cycle 5 of mass selection for adaptation to temperate environments beginning with Suwan-1(S)C6 as the C0 (Hallauer, 1994).
FS8A(T)C4 (M)C1	Cycle 1 of mass selection for earliness beginning with FS8A (T)C4(Horner, 1990) as the C0 (K.R. Lamkey, 1992, personal communication).
FS8B(T)C4 (M)C1	Cycle 1 of mass selection for earliness beginning with FS8B (T)C4(Horner, 1990) as the C0 (K.R. Lamkey, 1992, personal communication).
Mexican dent	A synthetic composed primarily of Tuxpeño and early U.S. Corn Belt germplasm (Michelini and Hallauer, 1993; Gerrish, 1983).
Mo17W(H27) C2	Cycle 2 of half-sib selection for standability using root pulling strength in Mo17W, a white synthetic made up of 14 versions of Mo17 that were in various stages of conversion to white endosperm (Gerdes et al., 1993).
MoSCSS(R19) C2	Cycle 2 of reciprocal recurrent selection in MoSCSS using Mo17 Elite Synthetic as a tester. MoSCSS was formed from 14 lines that were either directly developed from various cycles of Iowa Stiff Stalk Synthetic or were related versions of the original BSSS lines (Gerdes et al., 1993).
NB(K)RF5	Cycle 5 of reciprocal full-sib selection in Nebraska syn. B using Nebraska syn. K as a tester (West et al., 1980).
NB(S)RF7	Cycle 7 of reciprocal full-sib selection in Nebraska syn. B using Nebraska Stiff Stalk Synthetic as a tester (West et al., 1980).
NK(B)RF5	Cycle 5 of reciprocal full-sib selection in Nebraska syn. K using Nebraska syn. B as a tester (West et al., 1980).
NS(B)RF7	Cycle 7 of reciprocal full-sib selection in Nebraska Stiff Stalk Synthetic using Nebraska syn. B as a tester (West et al., 1980).
RSSSC(C6)	Cycle 6 of reciprocal selection using an inbred tester in an Illinois high-yield environment beginning with RSSSC, derived from Iowa Stiff Stalk Synthetic (R.J. Lambert, 1992, personal communication).
TROPHY L.M.	A low moisture selection made in North Carolina from TROPHY (a tropical hybrid composite) (Gerdes et al., 1993).
LH195	B37, B73 (Gerdes et al., 1993).
LH212	C123, LH123 (Gerdes et al., 1993).
LH216	LH123, Mo17 (Gerdes et al., 1993).

dominant alleles in P_y not present in I_1 or I_2. If P_y is to be used to improve I_1, which is the case when P_y is more closely related to I_1 than to I_2, then the difference $l\bar{p}_i\mu - j\bar{q}_j\mu$ is a measure of the net value of P_y as a donor (Bernardo, 1990a,b) and has been used as an indicator of whether to self directly from the F_1 of $P_y \times I_1$ or to backcross to I_1 prior to selfing. If the net value is not different from 0, it is maximum, and selfing in the $P_y \times I_1$ cross is indicated. If net value is significantly less than 0, then backcrossing to the inbred parent is recommended. Relationship values are derived from the equation $(I_2 \times P_y) - (I_1 \times P_y) + 0.5\ (I_1 - I_2)$. If the relationship is positive and significant, then P_y is more closely related to I_1 than to I_2; if it's negative and significant, P_y is more closely related to I_2.

In this study, $l\bar{p}_i\mu$, $j\bar{q}_j\mu$, $k\bar{q}_i\mu$, and relationship values were estimated for each of three different target hybrids: LH195 × LH212, LH195 × LH216, and LH212 × LH216. Standard errors for each statistic were calculated using the usual equations for the variance of a linear function, and an estimate was considered significantly different from zero if it exceeded twice its standard error.

RESULTS AND DISCUSSION

Grain Yield

Mean yields for all hybrids in an environment varied from 3.5 to 10.6 t ha^{-1} and for inbreds from 1.8 to 5.5 t ha^{-1} (Table 2). The Iowa environments in 1993 had extremely low yields because of cool wet weather. However, yields in Illinois in 1993 and in both Illinois and Iowa in 1994 were above average. Significant genotype × environment interactions (GE) for grain yield were found in both the hybrid and inbred trials. Because of the extreme variation in yields between the 1993 Iowa locations and the other environments, the GE sums of squares were subdivided into the portion due to interactions with 1993 Iowa environments, other environments, and 1993 Iowa vs. other environments. Percentage of the GE sum of squares accounted for by the interaction with 1993 Iowa vs. other environments was 22.6 for the hybrids and 35.0 for the inbred study. Within the other environments, interactions accounted for 62.5% of the total GE sum of squares for the hybrids and 58.4% for the inbreds. Because the GE resulting from differences between the high- and low-yielding environments was a relatively small proportion of the total, means across all environments were used for the analysis.

Because each population was crossed to each inbred, the analysis of variance among population crosses was subdivided into populations, inbreds, and the population × inbred interaction. Significant differences among populations and among inbreds were found for all traits. Significant population × inbred interactions (a measure of specific combining ability) were found only for grain yield, plant height, and ear height. Significant interactions were expected because certain populations, based on pedigree, were expected to be more closely related to one inbred than to another.

Relationship values based on grain yield data generally agree with expectation based on pedigree (Table 3). Inbreds LH212 and LH216 have one parent in common. Thus, populations related to LH195 in the cross LH195

Table 2. Planting dates and trial means for maize hybrids and inbreds in each environment included in the evaluation study.

Environment	Planting date	Grain yield	Grain moisture	Plant height	Ear height	Days to mid-silk
		t ha^{-1}	g kg^{-1}	cm		d
				Hybrid means		
Ames, IA, 1993	15 May	3.5	340	–	–	86.5
Ankeny, IA, 1993	20 May	5.0	255	217.7	114.9	–
Crawsfordsville, IA, 1993	14 May	4.8	228	237.5	126.6	–
Martinsburg, IA, 1993	18 May	5.0	234	237.8	127.3	–
Ames, IA, 1994	20 April	9.4	216	242.8	125.8	88.4
Fairfield, IA, 1994	21 April	9.9	195	259.8	139.0	–
Urbana-1, IL, 1993	10 May	8.1	268	235.9	113.1	74.3
Urbana-1, IL, 1994	26 April	9.8	279	217.8	111.9	83.2
Urbana-2, IL, 1993	12 May	7.8	246	237.5	121.0	–
Urbana-2, IL, 1994	18 May	10.6	257	237.8	116.2	64.5
Whiteland, IA, 1993	20 May	8.2	247	–	–	–
				Inbred means		
Ames, IA, 1993	15 May	2.1	333	–	–	89.0
Ankeny, IA, 1993	20 May	3.2	205	154.8	68.2	–
Crawsfordsville, IA, 1993	14 May	2.2	185	161.1	72.6	–
Martinsburg, IA, 1993	18 May	1.8	213	156.9	68.9	–
Ames, IA, 1994	20 April	5.5	214	174.3	78.6	94.9
Fairfield, IA, 1994	21 April	4.6	164	175.6	82.4	–
Urbana-1, IL, 1993	10 May	3.4	251	166.0	77.0	80.1
Urbana-1, IL, 1994	26 April	5.0	270	152.3	77.0	91.3
Urbana-2, IL, 1993	12 May	4.2	236	171.6	71.8	–
Urbana-2, IL, 1994	18 May	4.8	252	153.0	70.1	73.0
Whiteland, IN, 1993	20 May	4.4	256	–	–	–

× LH212 are likely to be related to LH195 in the cross LH195 × LH216. Of the 20 populations, RBS10(C6), BS28, FS8B(T)C4(M)C1, NB(K)RF5, and TROPHY L.M. showed no significant relationship to any of the inbreds. The backgrounds of these populations suggest they may represent different heterotic groups than any of the three inbreds. Because of significant positive relationship values for the crosses LH195 × LH216 and LH212 × LH216, and nonsignificant values for LH195 × LH212, populations B84R(H15)C1, BS11(FR)C10, BS17(CB)C4, NB(S)RF7, NS(B)RF7, and RSSSC(C6) were not related to LH216 but were equally related to LH195 and LH212. The MoSCSS(R19)C2 populations

Table 3. Relationship values† based on grain yield for each maize hybrid to be improved.

	Hybrid to improve		
Population	LH195 × LH212	LH195 × LH216	LH212 × LH216
B84R(H15)C1	0.07	1.06‡	0.98‡
RBS10(C6)	– 0.26	0.23	0.50
BS11(FR)C10	– 0.07	0.76‡	0.82‡
BS16(CB)C4	– 0.69‡	0.08	0.77‡
BS17(CB)C4	0.55	1.28‡	0.73‡
BS26	– 1.32‡	– 0.79‡	0.54
BS27	– 0.82‡	– 0.18	0.64
BS28	– 0.04	0.18	0.21
BS29	– 0.75‡	– 0.33	0.41
FS8A(M)C4	0.77‡	1.46‡	0.68‡
FS8B(M)C4	– 0.12	– 0.04	0.07
Mexican dent	– 0.47	0.32	0.79‡
Mo17W(H27)C2	– 0.99‡	– 2.00‡	– 1.01‡
MoSCSS(R19)C2	1.70‡	2.21‡	0.51
NB(K)RF5	– 0.42	– 0.15	0.27
NB(S)RF7	– 0.04	0.88‡	0.91‡
NK(B)RF5	– 0.78‡	– 0.07	0.71‡
NS(B)RF7	– 0.35	0.91‡	1.26‡
RSSSC(C6)	0.05	0.96‡	0.91‡
TROPHY L.M.	– 0.39	– 0.15	0.24

† Positive values indicate population more closely related to I_1; negative values indicate population more closely related to I_2.
‡ Value is at least twice the standard error.

showed a relationship to LH195 in two target hybrids but not to LH212 or LH216. The BS16(CB)C4 and NK(B)RF5 populations were more closely related to LH212 than to LH195 or LH216 and equally related to LH195 and LH216. The BS27 and BS29 populations were more closely related to LH212 in the LH195 × LH212 hybrid but showed no significant relationships in the other hybrids. The FS8A(T)C4(M)C1 population

Table 4. Mean grain yield and days to mid-silk for population × inbred maize crosses, target hybrids, and inbreds averaged across all environments (11 for yield, 5 for days to mid-silk).†

	Grain yield			Days to mid-silk		
Population	LH195	LH212	LH216	LH195	LH212	LH216
	t ha^{-1}			d		
B84R(H15)C1	6.82	7.39	7.32	81.2	78.5	79.4
RBS10(C6)	7.63	7.86	7.31	81.3	78.1	79.2
BS11(FR)C10	7.17	7.60	7.37	81.1	77.9	77.6
BS16(CB)C4	7.61	7.42	7.14	78.2	76.7	78.2
BS17(CB)C4	6.62	7.66	7.34	80.5	77.7	77.4
BS26	7.56	6.73	6.22	79.9	77.0	78.8
BS27	7.27	6.94	6.53	79.7	76.8	78.3
BS28	6.97	7.43	6.59	78.5	76.8	77.5
BS29	8.10	7.85	7.21	81.9	79.0	80.4
FS8A(T)C4	7.23	8.50	8.13	83.5	79.5	81.1
FS8B(T)C4	7.81	8.19	7.21	83.4	81.0	82.3
Mexican dent	7.31	7.33	7.07	78.8	75.9	76.2
Mo17W(H27)C2	7.79	7.30	5.24	81.1	78.1	80.2
MoSCSS(R19)C2	6.15	8.35	7.81	81.3	78.1	78.7
NB(K)RF5	7.74	7.82	7.04	81.1	78.6	80.5
NB(S)RF7	7.55	8.01	7.87	80.0	77.6	78.6
NK(B)RF5	7.91	7.63	7.29	80.6	78.1	79.4
NS(B)RF7	7.49	7.64	7.85	81.3	78.7	79.3
RSSSC(C6)	7.48	8.03	7.89	81.6	78.7	79.2
TROPHY L.M.	7.82	7.93	7.12	81.3	79.2	80.3
LH195	–	9.20	8.57	–	79.5	81.7
LH212	–	–	6.93	–	–	78.7
SE†	0.21	0.21	0.21	0.4	0.4	0.4
Inbred per se	3.79	4.78	2.68	86.8	83.7	86.4
SE‡	0.22	0.27	0.22	0.6	0.6	0.6

† Standard error of a hybrid mean.
‡ Standard error of an inbred mean.

Table 5. The $l\bar{p}_i\mu$ and $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$ values for grain yield for each target maize hybrid.

Population	LH195 × L1212 $l\bar{p}_i\mu$	$j\bar{q}_j\mu$ or $k\bar{q}_k\mu$	LH195 × LH216 $l\bar{p}_i\mu$	$j\bar{q}_j\mu$ or $k\bar{q}_k\mu$	LH212 × LH216 $l\bar{p}_i\mu$	$j\bar{q}_j\mu$ or $k\bar{q}_k\mu$
			kg ha^{-1}			
B84R(H15)C1	0.20	1.11†‡	0.45†	1.07†‡	0.77†	0.57†
RBS10(C6)	0.44†	1.22†‡	0.72†	1.36†‡	1.00†	0.81†
BS11(FR)C10	0.30†	1.32†‡	0.55†	1.15†‡	0.87†	0.65†
BS16(CB)C4	0.26†	1.06†‡	0.72†	1.43†‡	0.78†	0.68†
BS17(CB)C4	0.32†	1.09†‡	0.40†	1.02†‡	0.90†	0.70†
BS26	0.08	0.90†‡	0.63†	1.14†‡	0.44†	0.79†
BS27	0.06	1.02†‡	0.54†	1.20†‡	0.54†	0.74†
BS28	0.22	1.34†‡	0.39†	1.39†‡	0.79†	0.96†
BS29	0.49†	1.04†‡	0.96†	1.20†	1.00†	0.86†
FS8A(T)C4	0.69†	1.04†‡	0.75†	0.97†	1.32†	0.72†‡
FS8B(T)C4	0.60†	1.30†‡	0.81†	1.20†‡	1.17†	1.03†
Mexican dent	0.17	1.12†‡	0.56†	1.32†‡	0.74†	0.67†
Mo17W(H27)C2	0.28†	0.98†‡	0.45†	0.84†‡	0.72†	0.54†
MoSCSS(R19)C2	0.38†	0.80†‡	0.40†	0.78†‡	1.25†	0.81†‡
NB(K)RF5	0.42†	1.14†‡	0.78†	1.20†‡	0.98†	0.93†‡
NB(S)RF7	0.51†	1.34†‡	0.77†	1.12†‡	1.08†	0.61†
NK(B)RF5	0.39†	1.04†‡	0.87†	1.20†‡	0.89†	0.71†‡
NS(B)RF7	0.33†	1.18†‡	0.75†	1.11†‡	0.95†	0.49†‡
RSSSC(C6)	0.52†	1.11†‡	0.75†	1.09†‡	1.09†	0.61†‡
TROPHY L.M.	0.47†	1.16†‡	0.82†	1.20†‡	1.04†	0.94†

† Value greater than or equal to twice the standard error.
‡ Difference of $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$ from $l\bar{p}_i\mu$ greater than or equal to twice the standard error.

Table 6. The $l\bar{p}_i\mu$ and $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$ values for plant and ear height by target maize hybrid.

Population	LH195 × L1212 $l\bar{p}_i\mu$	$j\bar{q}_j\mu$ or $k\bar{q}_k\mu$	LH195 × LH216 $l\bar{p}_i\mu$	$j\bar{q}_j\mu$ or $k\bar{q}_k\mu$	LH212 × LH216 $l\bar{p}_i\mu$	$j\bar{q}_j\mu$ or $k\bar{q}_k\mu$
			cm			
			Ear height			
B84R(H15)C1	9.07†	12.11†	12.97†	10.08†‡	10.71†	6.30†‡
RBS10(C6)	15.25†	10.74†‡	17.02†	12.60†‡	15.97†	7.50†‡
BS11(FR)C10	8.95†	9.25†	13.52†	10.08†‡	10.92†	5.96†‡
BS16(CB)C4	9.59†	9.96†	11.41†	11.87†	10.31†	7.46†
BS17(CB)C4	9.31†	11.71†	13.56†	10.08†‡	11.12†	6.12†‡
BS26	7.63†	7.16†	12.12†	11.73†	9.18†	5.61†‡
BS27	10.89†	8.65†	14.05†	11.89†	12.16†	6.67†‡
BS28	6.24†	8.71†	12.05†	10.08†	8.84†	5.34†‡
BS29	14.39†	7.53†‡	17.33†	10.55†‡	15.35†	6.58†‡
FS8A(T)C4	14.16†	11.43†‡	16.32†	10.08†‡	14.93†	7.17†‡
FS8B(T)C4	12.70†	7.94†‡	17.96†	13.28†‡	15.02†	5.62†‡
Mexican dent	7.25†	8.37†	8.87†	10.07†	7.97†	7.68†
Mo17W(H27)C2	9.96†	7.69†	11.18†	9.00†	10.43†	8.89†‡
MoSCSS(R19)C2	10.03†	11.35†	14.69†	10.08†‡	12.05†	5.91†‡
NB(K)RF5	12.01†	10.35†	17.00†	10.08†	14.19†	5.75†‡
NB(S)RF7	11.05†	7.93†	14.57†	10.01†‡	12.54†	6.45†‡
NK(B)RF5	15.34†	10.26†‡	19.69†	10.08†‡	17.21†	6.07†‡
NS(B)RF7	12.08†	6.99†‡	16.84†	11.83†‡	13.67†	5.40†‡
RSSSC(C6)	14.35†	12.06†‡	16.58†	10.08†‡	15.16†	7.13†‡
Trophy L.M.	10.81†	9.43†	16.05†	10.08†	13.12†	5.63†‡
			Plant height			
B84R(H15)C1	13.78†	21.58†	20.44†	16.53†‡	17.31†	11.09‡
RBS10(C6)	16.38†	19.58†	21.35†	19.79†‡	19.91†	12.79‡
BS11(FR)C10	12.45†	14.32†	20.04†	17.14†‡	16.05†	10.24‡
BS16(CB)C4	11.34†	17.68†‡	14.81†	16.38†	14.87†	14.43
BS17(CB)C4	10.99†	23.05†	17.30†	16.53†	14.52†	11.45
BS26	11.21†	14.23†	19.32†	17.57†	15.07†	9.98†
BS27	13.85†	17.96†‡	19.22†	18.56†	17.39†	12.39‡
BS28	10.32†	16.77†‡	18.65†	20.33†	14.29†	9.87†‡
BS29	16.65†	15.54†	23.19†‡	17.32†	20.18†	11.22‡
FS8A(T)C4	20.87†	21.63†‡	24.65†‡	20.65†	24.40†	13.98‡
FS8B(T)C4	17.68†	16.49†	24.79†	18.84†‡	21.21†	10.65‡
Mexican dent	8.12†	14.94†‡	14.35†	16.41†	11.65†	11.64
Mo17W(H27)C2	12.54†	13.64†	16.61†	12.94†‡	15.87†	10.31‡
MoSCSS(R19)C2	17.34†	22.17†‡	23.85†	16.53†‡	20.87†	11.25‡
NB(K)RF5	16.95†	21.15†‡	26.74†	16.53†	21.65†	9.14†‡
NB(S)RF7	15.48†	20.55†‡	25.28†	16.53†‡	20.18†	9.13†‡
NK(B)RF5	18.34†	14.76†	27.30†	18.96†‡	22.63†	9.55†‡
NS(B)RF7	15.13†	16.84†	22.91†	19.85†‡	18.83†	10.14‡
RSSSC(C6)	20.59†	21.97†‡	24.24†	20.85†‡	24.12†	14.11‡
TROPHY L.M.	12.19†	16.60†‡	21.16†	20.81†	16.48†	9.55†‡

† Value greater than or equal to twice the standard error.
‡ $l\bar{p}_i\mu$ differs from $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$ by at least twice the standard error.

was unique in showing significant relationships to both LH195 and LH212, while Mo17W(H27)C2 showed a significant relationship to both LH212 and LH216 but no relationship with LH195. Based on pedigree, LH195 × LH212 and LH195 × LH216 were expected to show similar results in terms of relationship values. However, the high yield of LH212 (Table 4) resulted in a relatively large effect on relationship values. For example, B84R(H15)C1 × LH195 was lower yielding than crosses to either LH212 or LH216. Thus, B84R(H15)C1 was expected to show relationship to LH195 for both the LH195 × LH212 and LH195 × LH216 hybrids. However, the higher yield of LH212 than LH216 resulted in a nonsignificant relationship value when LH195 × LH212 was the target hybrid. A similar result was found for NB(S)RF7, RSSSC(C6), and BS17(CB)C4.

In general, $l\bar{p}_i\mu$ values for grain yield increased as the yield of the target hybrids decreased (Tables 4 and 5). This is expected because the lower the yield of the target hybrid, the larger the number of loci lacking favorable alleles. When LH195 × LH212 was the target hybrid, $l\bar{p}_i\mu$ values for five populations [B84R(H15)C1, BS26, BS27, BS28, and Mexican Dent] were not significant. For the other two lower yielding, target hybrids, all populations had significant $l\bar{p}_i\mu$ values. Population FS8A(T)C4(M)C1 had the largest $l\bar{p}_i\mu$ values when LH195 × LH212 or LH212 × LH216 was the target hybrid. However, BS29 had the largest $l\bar{p}_i\mu$ value when LH195 × LH216 was the target hybrid. The second and third largest $l\bar{p}_i\mu$ values when LH195 × LH212 was the target hybrid were from FS8B(T)C4(M)C1 and RSSSC(C6); when LH195 × LH216 was the target hybrid, NK(B)RF5 and TROPHY L.M. were second and third; when LH212 × LH216 was the target hybrid, MoSCSS(R19)C2 and FS8B(T)C4 were second and

third. In general, target hybrids LH195 × LH212 and LH212 × LH216 ranked the populations similarly with larger disagreements in ranking between these two hybrids and LH195 × LH216.

As $l\bar{p}_i\mu$ values became larger, across target hybrids, the need for backcrossing decreased as evidenced by a significant difference between $l\bar{p}_i\mu$ and $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$ (Table 5). For all populations, when LH195 × LH212 was the target hybrid, a need for backcrossing at least once before selfing was indicated. When LH212 × LH216 was the target hybrid, none of the populations would have required backcrossing. In some cases, $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$ values were significantly larger than $l\bar{p}_i\mu$ values, indicating the population × line cross being tested yielded more than the target hybrid. This result stresses the importance of choosing an elite target hybrid. In retrospect, LH212 × LH216 may have been an unrealistic choice as a target hybrid. It is not used commercially because of its performance and the relationship between the lines.

Table 7. Mean plant and ear heights for population × inbred crosses target hybrids and inbreds averaged across seven environments.

Population	Plant height			Ear height		
	LH195	LH212	LH216	LH195	LH212	LH216
			cm			
B84R(H15)C1	222.7	238.1	236.6	110.1	118.4	122.1
RBS10(C6)	231.9	243.3	238.4	125.2	130.8	130.2
BS11(FR)C10	234.5	235.5	235.8	115.5	118.2	123.2
BS16(CB)C4	225.6	233.3	225.0	115.4	119.5	119.0
BS17(CB)C4	214.1	232.6	230.3	111.3	118.9	123.3
BS26	232.2	233.0	234.3	117.1	114.0	120.4
BS27	230.1	238.3	234.1	120.6	122.1	124.2
BS28	225.4	231.2	233.0	111.2	112.8	120.3
BS29	240.5	243.9	242.1	129.9	128.3	130.8
FS8A(T)C4	236.7	252.3	245.0	121.6	128.6	128.8
FS8B(T)C4	240.6	245.9	245.3	125.7	125.7	132.1
Mexican dent	224.6	226.8	224.2	113.9	114.8	113.9
Mo17W(H27)C2	236.1	235.3	221.7	120.7	119.7	116.3
MoSCSS(R19)C2	228.6	245.3	243.4	113.5	120.3	125.5
NB(K)RF5	229.9	244.5	249.2	119.5	124.3	130.1
NB(S)RF7	228.1	241.5	246.2	111.1	122.4	125.4
NK(B)RF5	245.4	247.3	250.3	126.3	131.0	135.5
NS(B)RF7	234.8	240.8	241.5	126.3	122.6	129.8
RSSSC(C6)	235.5	251.8	244.2	120.7	129.0	129.3
TROPHY L.M.	229.4	235.0	238.0	118.9	121.9	128.2
LH195	–	238.3	228.7	–	116.1	116.3
LH212	–	–	224.1	–	–	113.3
SE†	2.0	2.0	2.0	1.7	1.7	1.7
Inbred per se	143.1	182.9	162.6	61.9	84.4	76.0
SE‡	2.3	2.3	2.3	1.3	1.3	1.3

† Standard error of a hybrid mean.
‡ Standard error of an inbred mean.

Table 9. Mean protein and starch concentrations for maize population × inbred crosses, target hybrids, and inbreds averaged across four environments.

Population	Protein			Starch		
	LH195	LH212	LH216	LH195	LH212	LH216
			g kg^{-1}			
B84R(H15)C1	10.3	9.6	10.0	64.7	65.2	64.8
RBS10(C6)	10.1	9.7	10.1	64.9	64.8	64.2
BS11(FR)C10	10.1	9.5	10.3	64.6	65.1	64.1
BS16(CB)C4	10.8	10.0	10.5	63.8	64.5	64.2
BS17(CB)C4	10.2	9.7	9.7	64.2	64.7	64.4
BS26	10.3	9.6	10.5	65.0	65.8	64.4
BS27	10.4	9.8	10.5	64.4	64.9	64.0
BS28	10.9	10.1	10.6	63.6	64.2	63.8
BS29	10.9	10.2	10.3	63.9	64.5	64.0
FS8A(T)C4	10.7	9.5	10.2	63.7	65.4	64.6
FS8B(T)C4	10.6	9.2	10.2	64.3	64.8	64.5
Mexican dent	10.7	9.8	10.5	64.9	65.3	63.9
Mo17W(H27)C2	10.3	9.6	10.0	64.8	65.3	64.3
MoSCSS(R19)C2	10.0	9.4	9.8	64.6	65.4	64.4
NB(K)RF5	10.1	9.6	9.8	64.9	65.1	64.5
NB(S)RF7	9.9	9.6	10.1	64.8	65.3	64.3
NK(B)RF5	10.6	9.8	10.5	64.0	64.9	63.8
NS(B)RF7	10.1	9.5	10.3	64.9	65.1	64.4
RSSSC(C6)	10.1	9.4	9.9	64.6	64.8	64.5
TROPHY L.M.	10.7	10.3	11.0	64.3	64.7	63.6
LH195	–	9.4	9.8	–	65.8	65.1
LH212	–	–	9.6	–	–	65.0
SE†	0.2	0.2	0.2	0.3	0.3	0.3
Inbred per se	11.6	10.4	10.8	63.5	63.8	63.8
SE‡	0.1	0.1	0.1	0.9	0.9	0.9

† Standard error of a hybrid mean.
‡ Standard error of an inbred mean.

Plant and Ear Height

For plant and ear height, alleles for greater height are usually dominant. However, breeders usually desire shorter plants and lower ear height. Thus, recessive alleles are favorable, and the difference $j\bar{q}_j\mu - l\bar{p}_i\mu$ measures net value of a population for plant or ear height (Dudley, 1988a) if I_1 is the line to be improved and $k\bar{q}_k\mu - l\bar{p}_i\mu$ if I_2 is the line to be improved. The choice of a line to improve is based on results for grain yield.

For all three target hybrids, FS8A(T)C4(M)C1 and RSSSC(C6) had significantly more unfavorable dominant alleles than favorable recessives for both plant and ear height (Table 6), suggesting attention would need to be given to plant and ear height if these populations were used to improve any of the three lines. None of the populations had significantly more favorable recessive alleles than unfavorable dominants for ear height. However, when LH195 × LH212 was the target hybrid,

Table 8. The $l\bar{p}_i\mu$ and $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$ values for days to mid-silk for each target hybrid. Negative values indicate dominance for earliness.

Population	LH195 × L1212		LH195 × LH216		LH212 × LH216	
	$l\bar{p}_i\mu$	$j\bar{q}_j\mu$ or $k\bar{q}_k\mu$	$l\bar{p}_i\mu$	$j\bar{q}_j\mu$ or $k\bar{q}_k\mu$	$l\bar{p}_i\mu$	$j\bar{q}_j\mu$ or $k\bar{q}_k\mu$
				d		
B84R(H15)C1	−1.59†	−1.05†	−1.98†	−0.82†‡	−1.38†	−1.75†
RBS10(C6)	−1.73†	−2.61†‡	−2.03†	−0.74†‡	−1.54†	−1.78†
BS11(FR)C10	−1.85†	−2.61†‡	−2.49†	−0.40‡	−1.73†	−1.18†
BS16(CB)C4	−2.48†	−1.81†	−2.92†	−1.17†‡	−2.26†	−2.03†
BS17(CB)C4	−1.98†	−1.05†‡	−2.66†	−0.50†‡	−1.83†	−1.21†
BS26	−2.34†	−2.52†	−2.47†	−1.55†‡	−2.12†	−2.17†
BS27	−2.45†	−2.53†	−2.63†	−1.61†‡	−2.23†	−2.06†
BS28	−2.41†	−1.90†	−3.13†	−1.02†‡	−2.19†	−1.62†
BS29	−1.32†	−2.52†‡	−1.56†	−1.66†	−1.10†	−1.96†‡
FS8A(T)C4	−0.84†	−0.82†	−0.98†	−0.68†	−0.86†	−2.09†‡
FS8B(T)C4	−0.32	−2.24†‡	−0.73†	−1.55†‡	−0.10	−1.90†‡
Mexican dent	−2.89†	−2.53†	−3.38†	−0.63†‡	−2.67†	−1.45†‡
Mo17W(H27)C2	−1.76†	−2.51†	−1.82†	−1.48†	−1.54†	−1.27†
MoSCSS(R19)C2	−1.72†	−1.02†‡	−2.12†	−0.62†	−1.54†	−1.56†
NB(K)RF5	−1.53†	−2.31†	−1.73†	−1.41†	−1.31†	−2.24†‡
NB(S)RF7	−2.02†	−2.27†	−2.49†	−0.91†‡	−1.81†	−1.77†
NK(B)RF5	−1.75†	−2.30†	−2.13†	−1.58†	−1.53†	−1.90f
NS(B)RF7	−1.49†	−2.35†‡	−1.99†	−0.79†‡	−1.27†	−1.60†
RSSSC(C6)	−1.48†	−1.05†	−1.93†	−0.68†‡	−1.27†	−1.55†
TROPHY L.M.	−1.24†	−2.13†‡	−1.75†	−1.53†	−1.02†	−1.82†

† Values greater than or equal to twice the standard error.
‡ $l\bar{p}_i\mu$ different from $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$ by at least twice the standard error.

Table 10. The $l\bar{p}_l$ and $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$ values for protein and starch for each target hybrid. Negative values indicate dominance for low protein or starch; positive values indicate dominance for high protein or starch.

Population	LH195 × L1212 $l\bar{p}_l\mu$	LH195 × L1212 $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$	LH195 × LH216 $l\bar{p}_l\mu$	LH195 × LH216 $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$	LH212 × LH216 $l\bar{p}_l\mu$	LH212 × LH216 $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$
				g kg⁻¹		
				Protein		
B84R(H15)C1	−0.17†	−0.60	−0.13	−0.27	−0.21‡	−0.42
RBS10(C6)	−0.12	−0.26	−0.09	−0.29	−0.15	−0.42†
BS11(FR)C10	−0.21‡	−0.57†	−0.03	−0.32†	−0.15	−0.51†
BS16(CB)C4	0.06	−0.65†	0.10	−0.27†	0.02	−0.41†
BS17(CB)C4	−0.12	−0.26	−0.28‡	−0.49	−0.17	−0.21
BS26	−0.16	−0.59†	0.05	−0.33†	−§	−
BS27	−0.07	−0.26	0.07	−0.28†	−0.04	−0.47†
BS28	0.08	−0.69†	0.13	−0.27†	0.05	−0.42†
BS29	0.13	−0.60†	0.01	−0.54†	0.07	−0.21†
FS8A(T)C4	−0.22‡	−0.88†	−0.05	−0.53†	−0.19‡	−0.48†
FS8B(T)C4	−0.31‡	−0.92†	−0.07	−0.50†	−	−
Mexican dent	−0.07	−0.71†	0.11	−0.27†	−0.04	−0.49†
Mo17W(H27)C2	−0.16	−0.59†	−0.14	−0.27	−0.20‡	−0.41
MoSCSS(R19)C2	−0.27‡	−0.58†	−0.27‡	−0.27	−0.32‡	−0.40
NB(K)RF5	−0.18	−0.26	−0.23‡	−0.27	−0.24‡	−0.35
NB(S)RF7	−0.18	−0.26	−0.16	−0.33	−0.19‡	−0.44†
NK(B)RF5	−0.08	−0.67†	0.09	−0.27†	−0.05	−0.48†
NS(B)RF7	−0.20	−0.26	−0.04	−0.30†	−0.15	−0.49†
RSSSC(C6)	−0.25‡	−0.59†	−0.19	−0.27	−0.27‡	−0.43
Trophy L.M.	0.21‡	−0.26†	0.28‡	−0.32†	0.22‡	−0.46†
				Starch		
B84R(H15)C1	0.15	0.43‡	0.18	0.34‡	0.31‡	0.16
RBS10(C6)	0.01	0.45‡†	0.05	0.17	0.04	0.14
BS11(FR)C10	0.11	0.45‡†	−0.03	0.21	0.11	0.05
BS16(CB)C4	−0.23	0.40‡†	−0.15	0.32‡†	−0.02	0.18
BS17(CB)C4	−0.11	0.44‡†	−0.01	0.34‡†	0.08	0.19
BS26	0.38‡	0.38‡	0.13	0.18	−	−
BS27	0.01	0.45‡†	−0.12	0.24†	0.03	0.07
BS28	−0.37‡	0.41‡†	−0.33‡	0.34‡†	−0.20	0.16
BS29	−0.22	0.43‡†	−0.21	0.40‡†	−0.06	0.15
FS8A(T)C4	−0.06	0.14	−0.08	0.17	0.30‡	0.10
FS8B(T)C4	−0.04	0.43‡†	0.02	0.34‡	0.14	0.17
Mexican dent	0.22	0.47‡	−0.03	0.09	−	−
Mo17W(H27)C2	0.22	0.44‡	0.06	0.21	0.22	0.04
MoSCSS(R19)C2	0.16	0.37‡	0.01	0.29‡	0.24	0.05
NB(K)RF5	0.13	0.55‡	0.13	0.22	0.19	0.12
NB(S)RF7	0.20	0.43‡	0.05	0.24	0.22	0.05
NK(B)RF5	−0.08	0.33‡†	−0.26‡	0.30‡†	0.00	0.03
NS(B)RF7	0.15	0.48‡	0.11	0.23	0.19	0.11
RSSC(C6)	0.02	0.48‡†	0.04	0.31‡	0.13	0.17
TROPHY L.M.	−0.08	0.48‡†	−0.24	0.17†	−0.13	0.04

† $l\bar{p}_l$ different from $j\bar{q}_j\mu$ or $k\bar{q}_k\mu$ by at least twice the standard error.
‡ Greater than twice the standard error.
§ Estimates of parameters not possible because of failure of assumptions in the model.

seven populations had significantly more favorable recessives for plant height. This agrees with the greater plant height of LH195 × LH212 than the other target hybrids (Table 7).

Flowering Date

Generally, genes for early flowering are dominant and earliness is desired; thus populations with the most negative $l\bar{p}_l\mu$ values have the most dominant favorable alleles for mid-silk date. Except for FS8B(T)C4(M)C1, all populations had significant $l\bar{p}_l\mu$ values for mid-silk date (Table 8). The three target hybrids generally ranked the populations the same. Six populations [RBS10(C6), BS11(FR)C10, BS29, FS8B(T)C4(M)1, NS(B)RF7, and TROPHY L.M.] had significantly fewer dominant favorable alleles than unfavorable recessive alleles, while BS17(CB)C4 and MoSCSS(R19) had significantly more

dominant alleles when LH195 × LH212 was the hybrid to improve (Table 8). Results when LH212 × LH216 was the target hybrid were similar to those of LH195 × LH212. Most populations had more favorable dominant alleles than unfavorable recessives when LH195 × LH216 was the target hybrid. This difference between LH195 × LH216 and the other hybrids results from later flowering of LH195 × LH216 (Table 4).

Moisture, Stalk Lodging, and Root Lodging

The procedure for identifying hybrids did not work well for these traits. Because most of the population target hybrid combinations had estimates of $\bar{q}_j$ or $\bar{q}_k$ outside the limits of 0 and 1, it was not possible to estimate $l\bar{p}_l\mu$ or the other parameters in the model. Thus, the assumptions on which the model is based were not met for these traits.

Chemical Composition

Of the three chemical constituents, only starch and protein gave usable results. Because dominance is for low protein (Table 9), protein was treated in the same manner as plant and ear heights, i.e., the relative number of favorable recessives was evaluated. For protein, 8 of the 20 populations [BS11(FR)C10, BS16(CB)C4, BS28, BS29, FS8A(T)C4(M)C1, MEXICAN DENT, NK(B)RF5, and TROPHY L.M.] had significantly more favorable recessive alleles than unfavorable dominant alleles, regardless of the target hybrid (Table 10).

For starch, where dominance is for high starch concentration (Table 10), only 6 of 60 $l\overline{p}_i\mu$ estimates were greater than twice the standard error and there was no consistency across target hybrids. Thus, none of the populations appear to have potential for increasing starch concentration in these hybrids.

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