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Expression of Heterosis in Leaming and Midland Corn Belt Dent Populations

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Successful maize (*Zea mays* L.) breeding programs are based on specific heterotic patterns. The Iowa Stiff Sralk Synthetic x Lancaster Sure Crop heterotic pattern is widely exploited in U.S. maize breeding programs. Alternative U.S. heterotic patterns have been suggested, but they have received limited attention and improvement. The objectives of this study were to evaluate cultivar crosses between Leaming and Midland Yellow Dent cultivars before and after inbred progeny selection and to assess their potential as an alternative U.S. heterotic pattern. Grain yield had a midparent heterosis value of 4.9% before selection and 17.8% in the third cycle of selection. The increase of grain yield heterosis (12.9%) through selection was highly significant (P ≤ 0.01), and crosses between S₁ generations showed an increased rate of inbreeding depression through selection. Grain moisture of the cross (20.1%) was significantly (P < 0.05) less than the Midland Yellow Dent (24.5%) cultivar but was not significantly greater than the Leaming (17.7%) cultivar. Root lodging strength was significantly improved through selection with 1.1% root lodging of the cross *after selection* (midparent heterosis value of −73.2%). Intrapopulation recurrent selection was successful for increasing the heterotic expression between Leaming and Midland Yellow Dent maize cultivars. An interpopulation recurrent selection program between the improved selection cycles Leaming and Midland Yellow Dent seems desirable.

INDEX DESCRIPTORS: *Zea mays* L., germplasm improvement, recurrent selection, inbred selection, heterotic patterns.

The heterosis concept in maize (*Zea mays* L.) was developed independently by E. M. East and G. H. Shull in the early 1900s (Shull 1952, Wallace and Brown 1956, Hayes 1963). The practical value of hybrid vigor traces back to the controlled hybridization of Southern Dents and Northern Flints by U.S. farmers in the nineteenth century (Enfield 1866, Leaming 1883, Brown 1950, Anderson and Brown 1952). It was realized that genetic divergence of parental crosses was important for hybrid vigor expression (Collins 1910), but the expression of heterosis also depended on the range of genetic divergence (Moll et al. 1965). Based on these earlier observations, one of the more difficult tasks was to predict heterotic responses between unrelated genotypes. Modern research approaches based on biochemical assays (Smith et al. 1985a,b) or DNA marker data (Dudley 1993, Stuber 1994, Labate et al. 1997, Melchinger 1997) have been useful to assess genetic diversity and genetic divergence. They are of limited usefulness, however, for predicting good heterotic combinations. These studies were not successful because of other population properties, such as the importance of dominance genetic effects (Falconer and Mackay 1996) and consistent linkages between DNA markers and quantitative trait loci (QTLs) for performance (Dudley 1993). Evaluation of the performance of crosses among groups based on genetically diverse parents is essential to identify promising heterotic patterns (Melchinger 1997).

Heterotic patterns (crosses between known genotypes that express a higher level of heterosis) became established by relating the heterosis of crosses with the origin of the parents included in the crosses (Hallauer et al. 1988). The data suggested that hybrids of lines from different germplasm sources had greater yields than hybrids of lines from similar sources. Because these studies were restricted to inbred lines from few germplasm sources, only the Reid Yellow Dent ×

Lancaster Sure Crop and Iowa Stiff Stalk Synthetic × Lancaster Sure Crop heterotic patterns were fully developed. Other heterotic groups were available, but they were identified later and have the disadvantage of having poorer agronomic traits (Goodman 1985). Tsotsis (1972) and Kauffman et al. (1982) reported one of the few studies of possible alternative U.S. heterotic patterns. They analyzed diallel crosses among nine U.S. Corn Belt open-pollinated varieties and found that there were specific heterotic combinations that performed better than cross between Reid Yellow Dent and Lancaster Sure Crop. They concluded that Leaming × Midland Yellow Dent was a potential heterotic pattern. Both parental populations, however, needed improvement to meet current standards of germplasm included in breeding programs.

Three cycles of inbred progeny selection were conducted in Leaming and Midland Yellow Dent populations. The objectives of this research were to evaluate the heterotic expression between Leaming and Midland Yellow Dent populations before and after inbred progeny selection and to assess their potential as an alternative U. S. heterotic pattern.

METHODS

Leaming and Midland Yellow Dent maize populations were included in a long-term breeding program. Three cycles of inbred progeny recurrent selection based on S₁ and S₂ progenies were performed in each population. Carena and Hallauer (2001) described the populations and details of the selection and evaluation programs.

The original populations and their interpopulation crosses corresponding to cycles 0 and 3 were evaluated at two levels of inbreeding (F = 0 and F = 0.5) in five Iowa environments. Data were collected on 10 traits. Stand counts (M ha⁻¹) were taken after plots were thinned to a maximum plant density of 67,000 plants ha⁻¹. Days to anthesis (days from planting to pollen shedding by 50% of the plants within a plot) and days to silking (days from planting to silks

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Table 1. Means of eight traits for Leaming and Midland Yellow Dent maize cultivars and crosses and their comparisons with selection cycles and checks.

Genotype	Grain		Stand	Lodging		Dropped ears	Plant height	Ear height
	Yield	Moisture		Root	Stalk			
	Mg ha⁻¹	%	M ha⁻¹	------------------ % ------------------		------------- cm -------------		
Midland C0	2.88	26.0	58.6	29.4	15.6	4.5	249.7	138.6
Leaming C0	3.01	17.3	62.8	4.4	22.0	4.8	215.6	100.1
Leaming C0 × Midland C0	3.09	19.2	61.2	9.8	19.2	6.6	213.8	118.0
Leaming C0 × Midland C0 ⊗	1.74	19.4	54.4	8.5	20.0	5.8	208.0	99.8
Midland C1	2.89	25.0	58.3	13.0	21.6	2.2	232.7	122.6
Leaming C1	2.79	18.1	60.1	4.7	10.2	6.8	202.9	86.9
Midland C2	3.17	25.3	59.7	11.5	14.2	2.4	227.9	122.4
Leaming C2	2.99	17.0	62.2	3.5	14.3	5.3	201.8	84.4
Midland C3	3.19	24.5	62.1	6.3	17.9	2.6	217.7	107.1
Leaming C3	3.86	17.7	62.9	1.9	8.0	4.1	197.0	83.9
Leaming C3 × Midland C3	4.15	20.9	61.6	1.1	13.3	5.6	216.9	99.5
Leaming C3 × Midland C3 ⊗	2.19	19.4	55.5	3.3	15.7	4.3	191.4	84.8
BS21 (R) C6	4.35	17.9	62.8	0.3	6.2	5.2	190.7	83.7
BS22 (R) C6	4.90	17.2	63.2	0.5	3.1	1.9	181.1	74.6
BS28 (R) C1 Syn1	4.28	21.5	60.7	3.1	9.4	1.8	208.8	102.7
BS29 (R) C1 Syn1	5.06	24.2	59.2	2.8	13.5	3.7	221.1	113.7
BS10 (FR) C12 Syn1	5.80	21.1	63.6	2.4	13.5	4.0	229.9	115.1
BS11 (FR) C12 Syn1	5.94	20.4	63.0	1.7	13.0	2.8	240.0	118.8
LSD (0.05)	0.60	2.9	4.9	9.4	6.4	2.3	8.9	7.7

⊗ Entries after one generation of self-pollination.

being shown by 50% of the plants within a plot) were taken in only one location. Plant and ear height, root and stalk lodging, and dropped ears were measured at four locations. Plant height was as the average height (cm) of 10 competitive plants per plot, with height measured as the distance from the ground to the node of the flag leaf. Ear height was the average distance (cm) from the ground to the highest ear-bearing node of 10 competitive plants. Root lodging (percentage of plants leaning more than 30° from vertical), stalk lodging (percentage of plants broken at or below the ear node), and dropped ears (percentage of ears detached from plants) were measured before harvest. Grain yield (adjusted to a 15.5% grain moisture basis and expressed as Mg ha⁻¹), and grain moisture (%) were measured directly at five locations using combine sensors without gleaning for lodged plants and dropped ears.

Analyses of variance were performed for all traits for each location. Combined analyses of variance across locations were done for eight traits where environments and entries were considered random and fixed effects, respectively. The entry sum of squares was orthogonally partitioned for Leaming, Midland Yellow Dent, Leaming by Midland Yellow Dent, checks, and among group sources of variation. The genotype-by-environment interaction was subdivided according to the entry sum of squares partition to make appropriate F-tests. Leaming by Midland Yellow Dent source of variation represented the cross between the two maize populations before and after selection. Within this source of variation, the mean increase through selection was tested as well as its interaction with the change of inbreeding depression during selection.

Combined analyses of variance for all traits were also performed to detect significant heterotic expressions. Midparent heterosis values were estimated as the difference between the mean of a cross and the midparent value of its parents, divided by midparent value, and expressed as a percentage. Fisher's protected least significance difference (FLSD) was applied for mean comparisons (Carmer and Swanson

1971) among parents, midparent, and midparent heterosis values. Inbreeding depression was measured as a percentage of the noninbred generation before and after selection and expressed as a rate (Lamkey and Smith 1987). The entry means across environments were used for the generation mean analysis developed by Smith (1979a,b; 1983). This model provides estimates of the relative importance of heterosis in the cross between the original populations (HII') and changes in allelic frequencies and dominance effects for the cross between advanced cycles of the same populations (HQII'). Genetic parameters DLI'I and DLII' (representing the contribution of Leaming and Midland Yellow Dent to the change in the mean of the population cross, respectively) could not be estimated, and a joint effect of DLII', DLI'I, and HQII' was considered as the heterosis effect after selection (HASII'). All the experiments were analyzed by SAS (SAS 1989).

RESULTS AND DISCUSSION

Average grain yield across environments was 3.09 Mg ha⁻¹ for the cross between the nonselected populations compared with an average grain yield of 4.15 Mg ha⁻¹ after three cycles of intrapopulation selection (Table 1). The 34.3% increase was highly (P ≤ 0.01) significant (Table 2). This percentage was similar to 28.8% obtained from BSTL × BS2 after evaluating five cycles of inbred progeny selection (Iglesias and Hallauer 1991). A 28.2% grain yield increase for BS10 × BS11 was reported after four cycles of reciprocal full-sib recurrent selection (Eyhérabide and Hallauer 1991a), and a 16.5% yield improvement was observed after four cycles of reciprocal half-sib recurrent selection in BSSS × BSCB1 (Keeratinijakal and Lamkey 1993a). The change in midparent heterosis from selection, however, was not the same in the four breeding programs because inbred progeny selection did not cause a significant improvement of the midparent heterosis in BSTL × BS2 (Iglesias and Hallauer 1991)

Table 2. Subdivision of the sum of squares of the combined analyses of variance of eight traits for the cross between Midland Yellow Dent and Leaming maize populations evaluated in five Iowa environments.

Source of variation	d.f.	Mean squares								
		Grain				Lodging		Dropped ears	Plant height	Ear height
		Yield	Moisture	Stand	d.f.	Root	Stalk			
		Mg ha^{-1}	%	M ha^{-1}		%			cm	
L × M[a]	3	17.00**	9.05	214.29**	3	207.98*	117.12	10.40	3,418.39**	2,221.45**
Cross (C)[b]	1	8.47**	9.68	8.59	1	586.54*	310.67	17.24	2,972.03**	3,361.73**
Inbreeding (I)[c]	1	41.09**	7.14	632.35**	1	2.40	32.15	13.19	7,274.23**	3,265.35**
C × I	1	1.44	10.33	1.93	1	35.00	8.54	0.76	8.93	37.28
(L × M) × E[d]	12	0.34	5.72	17.24	9	57.21	75.10	15.44	71.17	38.15

*, **Significant at 0.05 and 0.01 probability levels, respectively.
[a]L = Leaming, M = Midland Yellow Dent.
[b]Mean difference of the cross between cycles 0 and 3.
[c]Changes in the effect of inbreeding before and after selection.
[d]E = Environment.

Table 3. Midparent heterosis values and mean comparisons of eight traits for the cross between Leaming by Midland Yellow Dent maize populations before inbred progeny selection evaluated in five Iowa environments.

Entry	Means							
	Grain		Stand	Lodging		Dropped ears	Plant height	Ear height
	Yield	Moisture		Root	Stalk			
	Mg ha^{-1}	%	M ha^{-1}	%			cm	
Leaming C0	3.01a	17.3a[a]	62.8a	4.4a	22.0a	4.8a	215.6a	100.1a
Midland C0	2.88a	26.0c	58.6a	29.4c	15.6a	4.5a	249.7d	138.6d
Midparent value	2.95a	21.7b	60.7a	16.9b	18.8a	4.7a	232.7c	119.3c
Leaming C0 × Midland C0	3.09a	19.3ab	61.2a	9.8ab	19.2a	6.6a	231.8bc	118.0bc
LSD$_{0.05}$	1.0	3.4	6.5	11.3	9.2	3.6	7.6	7.8
LSD$_{0.01}$	1.5	7.4	9.5	16.4	13.4	5.2	11.1	11.3
Heterosis (%)	4.9	−11.0	0.8	−42.0	2.0	40.4	−0.4	−1.1

[a]Means followed by the same letter are not significantly different at the 0.05 probability level (FLSD test).

in contrast with interpopulation selection programs. Selection within Leaming and Midland Yellow Dent, however, suggests inbred progeny selection within populations was effective for improving the heterotic expression for grain yield in the improved cross (Tables 3, 4). The contrasting results emphasize the relative importance of genetic background (choice of germplasm) over selection strategy.

The cross (4.15 Mg ha^{-1}) between selected cycles of Leaming and Midland Yellow Dent had the greatest grain yield of the entries evaluated and was statistically similar to the third cycle of the Leaming population and two of the six checks tested (Table 1). Midparent heterosis of 17.8% for the C3 × C3 cross was similar to the 19.5% average midparent heterosis reported by Hallauer and Miranda Fo (1988) in more than one thousand variety crosses. The increase in midparent heterosis for Leaming by Midland Yellow Dent heterosis (12.9%) was similar to the heterotic expression manifested by interpopulation programs after four cycles of selection (Table 5). The HASII' genetic parameter estimate from Smith's model, however, was not significantly different from zero for grain yield (Table 6). HASII' represents the linear and quadratic functions of the changes in allelic frequencies and dominance effects for the cross between Leaming and Midland Yellow Dent. Some possible hypotheses can be related with the lack of significance in HASII'. Directional dominance of a trait

is defined as the dominance of the genes concerned in that trait being preponderantly in one direction (Falconer and Mackay 1996); it is required for the expression of heterosis before and after selection. Nondirectional dominance does not seem to be important in Leaming × Midland Yellow Dent crosses because significant dominance effects in original populations (DOI estimates) and changes in allele frequencies and dominance effects (DLI estimates) after selection were important in both populations (Carena and Hallauer 2001). Moreover, the per cycle rate of inbreeding depression after three cycles of inbred progeny selection increased from 0.027 Mg ha^{-1} to 0.039 Mg ha^{-1}, a higher rate than the one observed after four cycles of reciprocal full-sib recurrent selection in BS10 × BS11 (Eyhérabide and Hallauer 1991a). The increase in heterosis also depends on the changes in allelic frequencies (Δp) in both populations. If Δp of one population is zero, HQII' is by definition also zero. In addition, selection can increase the frequency of favorable alleles for some grain yield loci, but it may not be adequate to counteract the negative effects of other loci controlling the trait, especially for fewer selection cycles. The more probable hypothesis for yield improvement in the cross is that inbred progeny selection selected different alleles with dominance effects in the Leaming population, considering that the Leaming population was the only one with a significant DLI estimate

Table 4. Midparent heterosis values and mean comparisons of eight traits for the cross between Leaming by Midland Yellow Dent maize populations after inbred progeny selection evaluated in five Iowa environments.

	Means							
	Grain			Lodging		Dropped	Plant	Ear
Entry	Yield	Moisture	Stand	Root	Stalk	ears	height	height
	Mg ha^{-1}	%	M ha^{-1}	------------------- % -------------------			-------- cm --------	
Leaming (S) C3	3.86ab[a]	17.7a	62.9a	1.9a	8.0a	4.1a	197.0a	83.9a
Midland (S) C3	3.19a	24.5c	62.1a	6.3a	17.9a	2.6a	217.7b	107.1b
Midparent value	3.53ab	21.1abc	62.5a	4.1a	13.0a	3.4a	207.4ab	95.5ab
Leaming C3 × Midland C3	4.15b	20.9ab	61.6a	1.1a	13.3a	5.6a	216.9b	99.5b
LSD$_{0.05}$	0.69	1.8	4.0	5.1	7.0	1.8	8.9	8.8
LSD$_{0.01}$	1.00	2.6	5.9	7.3	10.1	2.7	13.0	12.8
Heterosis (%)	17.8	−0.9	−1.4	−73.2	2.4	67.4	4.6	4.2

[a]Means followed by the same letter are not significantly different at the 0.05 probability level (FLSD test).

Table 5. Midparent (MP) heterosis for grain yield from nonselected and selected crosses reported in maize selection programs.

Population crosses	Grain yield		References
	MP	I†	
	------------------- % -------------------		
BS16(S)C0 × BS2(S)C0	8.0		Iglesias and Hallauer (1991)
BS16(S)C4 × BS2(S)C5	20.2	12.2	Iglesias and Hallauer (1991)
BSTL(S)C0 × BS2(S)C0	18.7		Iglesias and Hallauer (1991)
BSTL(S)C5 × BS2(S)C5	23.2	4.5	Iglesias and Hallauer (1991)
BS10(FR)C0 × BS11(FR)C0	2.5		Eyhérabide and Hallauer (1991a)
BS10(FR)C4 × BS11(FR)C4	19.7	17.2	Eyhérabide and Hallauer (1991a)
BSSS(R)C0 × BSCB1(R)C0	25.4		Keeratinijakal and Lamkey (1993a)
BSSS(R)C4 × BSCB1(R)C4	42.8	17.4	Keeratinijakal and Lamkey (1993a)
BS21(R)C0 × BS22(R)C0	1.0		Menz and Hallauer (1997)
BS21(R)C3 × BS22(R)C3	10.2	9.2	Menz and Hallauer (1997)
Leaming(S)C0 × Midland(S)C0	4.9		Carena and Hallauer (2001)
Leaming(S)C3 × Midland(S)C3	17.8	12.9	Carena and Hallauer (2001)

†Increase of heterosis after selection.

Table 6. Heterosis estimates for seven traits in Leaming by Midland Yellow Dent maize cultivar crosses after inbred progeny selection; adapted from the Smith model (Smith, 1983).

Trait	HII′	HASII′
Grain yield (Mg ha^{-1})	0.23	0.006
Grain moisture (%)	−2.79**	0.52
Root lodging (%)	−5.74**	1.26
Stalk lodging (%)	0.35	0.02
Dropped ears (%)	2.17*	0.31
Plant height (cm)	3.27	0.22
Ear height (cm)	−0.82	0.68

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

(Carena and Hallauer 2001). This seems to be a reasonable explanation because inbred progeny selection is based on the improvement of populations per se whereas interpopulation selection programs would select alleles contributing to the heterosis of the cross. The

hypothesis of selecting alleles that contribute to heterosis, however, was often associated with results from interpopulation programs based on nonsignificant HQII′ estimates (Eyhérabide and Hallauer 1991b, Keeratinijakal and Lamkey 1993b). Most studies have reported no heterosis improvement in grain yield based on the HQII′ estimate (Tanner and Smith 1987, Helms et al. 1989, Iglesias and Hallauer 1991, Eyhérabide and Hallauer 1991b, Keeratinijakal and Lamkey 1993b, Garay et al. 1996). Alternative models for detecting heterosis, therefore, would be advisable.

Average yield for the cross between nonselected (C0 × C0) populations was similar to the yields of the C0 cycles for both populations (Table 1). The midparent heterosis value of the original populations was not statistically significant (Table 3), which agrees with the nonsignificant HII′ estimate of Smith's model (Table 6). The small effect due to heterosis (HII′) in Leaming and Midland Yellow Dent population cross before selection is possibly associated with the lack of initial genetic divergence of alleles affecting grain yield because dominance was present in both populations. This observation in Leaming and Midland Yellow Dent populations was unexpected based on their heterotic combination (Kauffman et al. 1982) and their diverse geographic origins. We can speculate that negative het-

erotic contributions at certain loci from one population might have canceled positive responses at other loci from the other population. Lower midparent heterosis estimates have been reported in other genetic backgrounds (Eyhérabide and Hallauer 1991a, Menz and Hallauer 1997) and with significant HII' estimates (Iglesias and Hallauer 1991, Eyhérabide and Hallauer 1991b, Keeratinijakal and Lamkey 1993b, Garay et al. 1996). The relationship between additive and dominance genetic effects for grain yield in the cross between the original populations seems to be important. Dominance genetic effects in nonselected populations (DOI parameter in the Smith model) were more important for grain yield (Smith 1983, Oyervides-García and Hallauer 1986, Tanner and Smith 1987, Helms et al. 1989, Iglesias and Hallauer 1991, Eyhérabide and Hallauer 1991b, Stojšin and Kannenberg 1994, Garay et al. 1996). Keeratinijakal and Lamkey (1993b) showed, however, that additive genetic effects (AOI) were as important as dominance genetic effects in BSSS, and they found significant midparent heterosis when crossing BSSS and BSCB1 nonselected populations. Significant differences in allelic frequencies with additive and dominance effects, therefore, would be required for the expression of heterosis before selection. After selection, however, differences in allelic frequencies with dominance effects among populations should increase (Falconer and Mackay 1996, Hallauer 1999). Labate et al. (1997) have shown how successful selection can be in creating genetic divergence among populations, consequently, leading to a greater expression of heterosis.

Grain moisture had a significantly negative ($P \leq 0.01$) heterosis estimate (HII') before selection (Table 6). This result agrees with the genetic divergence reported in BSSS × BSCB1 for the same trait (Keeratinijakal and Lamkey 1993b). Midparent heterosis of the original cross was −11%, and the cross mean (19.2%) was statistically similar to Leaming (17.3%). Considering that grain moisture is a trait mainly associated with additive effects (Tanner and Smith 1987, Helms et al. 1989, Eyhérabide and Hallauer 1991b, Stojšin and Kannenberg 1994), the expression of heterosis was mostly dependent on the difference in allelic frequencies. A small amount of dominance, however, was reported in Midland Yellow Dent (Carena and Hallauer 2001). Grain moisture had a small positive change (1.6%) after three cycles of selection and was confirmed by the nonsignificant HASII' estimate, suggesting that the cross is adapted to Iowa environments (Tables 3, 4). Flowering dates, however, had a small negative trend through selection. A concern, though, was the 4-day difference between days to silk and days to pollen shedding that did not change through selection.

The HII' estimate was highly significant for root lodging, which disagrees with most studies (Eyhérabide and Hallauer 1991b, Keeratinijakal and Lamkey 1993b, Garay et al. 1996). Iglesias and Hallauer (1991) reported that genetic divergence for root lodging was expressed in more distant sources of germplasm, such as the cross between BS2 (ETO Composite) and BSTL (Tuxpeño × Lancaster). The highly significant HII' in Leaming by Midland Yellow Dent was represented in the −42% midparent heterosis expressed in the original cross. The root lodging difference between C0 and C3 changed from 9.8% to 1.1%. Dominance genetic effects for root lodging were present mainly in Midland Yellow Dent, and inbred progeny selection increased the frequency of favorable alleles of both populations. The nonsignificant estimate of HASII' suggests that selection was based on different alleles with dominance effects in both populations. Stalk lodging and dropped ears did not change significantly in the cross mean after selection (Table 2). But stalk lodging decreased 5.9% and dropped ears decreased 1.0% in the cross after selection. The significant HII' estimate for dropped ears was associated with its large midparent heterosis values (Tables 3, 4). The HASII' estimate of both traits was similar to zero as reported in other studies (Eyhérabide and Hallauer 1991b, Keeratinijakal and Lamkey 1993b,

Garay et al. 1996), but stalk lodging was reported to have significant HII' and HQII' estimates in the cross of BS2 × BSTL (Iglesias and Hallauer 1991).

Correlated mean changes in the cross between Leaming and Midland Yellow Dent were highly significant for plant and ear height (Table 2). The 18.5 cm reduction in ear height was greater than the 14.9 cm reduction in plant height and was mainly due to the change in the frequency of alleles with additive effects in the Leaming population, the shorter variety (Carena and Hallauer 2001). Inbreeding depression was highly significant for these traits (Table 2) and reduced their mean values. The lack of genetic divergence in the cross (HII') for plant and ear height was in agreement with their lower values of midparent heterosis before selection (Tables 3, 4). Keeratinijakal and Lamkey (1993b) reported highly significant HII' estimates for BSSS × BSCB1 for plant and ear height. The cross between Leaming and Midland Yellow Dent after selection did not produce any changes in heterosis (HASII' $\cong$ 0) for plant and ear height, which can be related to the relative importance of additive effects reported in these traits (Carena and Hallauer 2001). Ear height, however, had significant changes in allelic frequencies and dominance effects for BS2 × BSTL after five cycles of reciprocal half-sib recurrent selection (Iglesias and Hallauer 1991) and for BS10 × BS11 after eight cycles of reciprocal full-sib recurrent selection (Eyhérabide and Hallauer 1991b).

Inbred progeny selection was effective in improving the cross between Leaming and Midland Yellow Dent. Although the rate of inbreeding depression for grain yield increased after selection, midparent heterosis also increased, and its increase was similar to that of interpopulational recurrent selection programs. Grain yield heterosis among improved cycles of Leaming and Midland Yellow Dent populations is attributed to the selection of different alleles with dominance effects in Leaming populations. The increase of inbreeding depression in improved populations and crosses suggests that more loci were segregating for grain yield than in nonimproved populations, and that the frequency of favorable dominant alleles was increasing, although not significantly, if we restrict our results to the genetic parameters of the Smith model. Selection response of the cross has occurred at complementary loci because improvement in other traits was based on favorable attributes of both populations. The first objective of our long-term program has been achieved and considerable improvements have been made. We can conclude that further refinement is needed if Leaming and Midland populations are to become an alternative heterotic pattern in U.S. maize breeding programs. We propose the use of a reciprocal full-sib recurrent selection program to increase the efficiency of future selection for heterotic effects. Secondary characteristics such as stalk lodging and pollen-silk interval should be emphasized in future selection programs based on the Leaming × Midland Yellow Dent heterotic pattern.

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