COTTON IMPROVEMENT

Heterosis and Combining Ability of Cottons Originating From Different Regions of the United States

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INTERPRETIVE SUMMARY

Little use of heterosis "hybrid vigor" has been made in cotton in the United States. In cotton heterosis has the potential of increasing yield from 10 to 20% and of making improvements in fiber quality. Increased yield and fiber quality are vital to keeping U.S. cotton competitive with synthetics and foreign production. One of the problems in using heterosis in cotton is defining a strategy for the selection of parents that will ultimately produce productive hybrids. The objective of this study was to determine if the region of origin for parents was related to heterosis. To evaluate this hypothesis, we chose four parents from each of the four major cotton growing regions in the United States-East, Delta, Plains, and West. A set of 120 F₂ hybrids was produced and evaluated in three Missisippi Delta environments in 1990. Significant heterosis was detected for total lint yield at first harvest, lint percentage, boll weight, and fiber length. The analysis showed that to produce a high yielding F_2 population for a specific region, such as the Delta, at least one parent should be well-adapted to that region. For the second parent, no general trend was apparent that would result in superior hybrids. A possible exception would be the case where fiber quality was also a major breeding objective. In such a case, at least one parent should have above average fiber quality. Pedigree analyses and the diversity of molecular markers were inadequate for identifying parents that would be good parents for hybrids.

ABSTRACT

Exploiting heterosis is one method to increase cotton yields that have stagnated in recent years. We

produced 120 F2 cotton (Gossypium hirsutum L.) hybrids from a half diallel of 15 cultivars and one strain. The parents and their F2s (136 genotypes) were evaluated in three Mississippi Delta locations in 1990. Total and first harvest lint yields were taken from four replications per location. Yield components and fiber properties were determined from two replications. The primary objective of this study was to determine if parental region of origin was related to midparent and useful heterosis. We also explored the use of molecular markers (restriction fragment length polymorphisms, RFLPs) and coefficients of parentage in identifying heterotic effects. Significant heterosis over all crosses for total and first harvest yield, lint percentage, boll weight, and 50% span length were detected. For total vield, the specific combining ability and specific combining ability by location interaction components accounted for 79% of the total genetic variance components. General combining ability effects accounted for the remaining 21%. Four of the highest six general combiners for yield were from the Delta region. One each came from the East and West regions. The F₂s derived from the West's cultivar, Prema, were not only high in yield, but also resulted in the highest bundle strength. The correlation of genetic distance (calculated from RFLP data) and heterosis was 0.08, and that for coefficient of parentage and heterosis was 0.05. Region of origin for one parent of a cross was an important factor in the expression of F2 heterosis from crosses among Delta cultivars. But, a similar relationship with F2 heterosis in crosses between Delta cultivars and those from other regions was not observed. General approaches to producing high yielding F₂s are: (i) choose at least one parent well adapted to the targeted region; (ii) the second parent may come from any region or country; and (iii) if fiber quality is a breeding objective, at least one parent must have above average fiber quality as well as be a good yield combiner.

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Abbreviations: RFLP, restriction fragment length polymorphism.

Tsing heterosis to increase yield of cotton has long been an objective of breeders. Except in countries where a vast labor force is available to make emasculations and crosses by hand, no commercial use of heterosis currently exists in cotton (Chaudhry, 1997b). In India, at least 40% of cotton's production is derived from intraspecific hybrids of G. hirsutum, and 8% of its production is from G. hirsutum x G. barbadense L. hybrids (Chaudhry, 1997b). The yield increase of hybrids over the better parent or best commercial cultivar (useful heterosis) has been documented in numerous reviews (Loden and Richmond 1951; Davis 1978; Meredith 1984; Basu 1995). A review using more recent data (Meredith, 1998) showed an average useful heterosis of 21.4% (or 276 kg ha⁻¹) for F_1 hybrids, and 10.7% or (158 kg ha⁻¹) for F_2 s. These reviews conclusively show that both F_1 and F_2 hybrids can produce significantly higher yields than the current best yielding parent or commercial cultivar. Breeding research needs to address all possibilities to increase yield, including the use of heterosis. The average cotton yields for the United States and world have shown no increase since the early 1990s (Chaudhry, 1997a). Meredith et al. (1997) have reported that breeding progress for increased yield has greatly decreased in recent times.

The major limiting factor to using heterosis in cotton is the lack of an efficient, dependable crossing system. While numerous male sterile systems have been explored (Percy and Turcotte, 1991), male steriles and their restorer factors have often not been stable from environment to environment. Also, the genetics of the restorer factors to produce good "R" lines are complex. To avoid the inconsistency of results from male steriles and restorer factors and the cost of producing F_1 seed, the commercial use of F_2 hybrids has been proposed (Olvey, 1986). In the United States, Chembred released the first commercial F2 cultivars in 1992, but ceased operations in October 1995. Several factors contributed to the lack of F₂ commercial success. First, and perhaps the major factor, was the ineffectiveness of the male gametocide, TD-1123. The gametocide had to be applied every 14 to 21 days and, depending on the female's genotype, resulted in varying amounts of both male and female fertility. Incomplete male sterility resulted in nonhybrid seed and female sterility resulted in reduced yields. The carry-over effects of TD-1123 in the seed also reduced F_1 plant growth and yield the following year. The competitiveness of some F_2 cultivars produced using TD-1123 seemed to be less than the same F_2 s produced by hand crossing. To some, the lack of success by Chembred was the final chapter on the use of F_1 and/or F_2 hybrids in the United States.

However, several well-designed studies show the potential for using F_2 hybrids. Tang et al. (1993) evaluated yield performance of 64 F₂s from four environments. The design was a North Carolina II with four females crossed with 16 males. The females were commonly grown cultivars DES 119, Deltapine 50, Stoneville 453, and Coker 315. The males were lines that had shown good host-plant resistance to many cotton pests. The best male yield combiner was Delcot 344 that averaged 151 kg ha⁻¹ (11.8%) higher yields than the commercial cultivars. Weaver (1984) compared 66 F_1s and F_2s from a half-diallel with their parents. The average midparent heterosis for F_1 s and F_2 s was 13.2% (118 kg ha⁻¹) and 7.1% (6.3 kg ha⁻¹), respectively. He indicated certain F₂s such as Dixie King x Pope were as productive as the best F_1 hybrids.

Due to the genetic variation within an F_2 , the possibility exists that F₂s might have a broader range of adaptation than conventional cultivars. R.H. Sheetz (1997, personal communication) reported that, in his experience with F_2s , they tended to have a broader range of adaptation than did commercial cultivars and that they frequently showed their greatest superiority when grown under stress conditions. Reid (1995) reported that F₂ superiority over their best parents was only detected under stress conditions. These conditions were lower yielding Verticillium wilt (Verticillum dahliae_Kleb.) and nonirrigated environments. Bauer and Green (1996) also reported F₂s' greater superiority over parents was in the lower yielding sites. That $F_{2}s$ can also produce better combinations of yield and fiber quality than their parents has been demonstrated by Meredith (1990). In that study, F_2 performance was highly correlated (r = 0.86) with F_1 yield performance. Occasionally, F₂ heterosis equaled F₁ heterosis. The mean yield of Deltapine 16, Stoneville 603, their F_1 , and F_2 populations were 856, 862, 920, and 940 kg ha⁻¹, respectively (Meredith and Bridge, 1972).

Breeders of all crops that use heterosis have the challenge of finding good combiners; cotton is no exception. The general approach is to cross genetically unrelated cultivars, but no information is apparent as how to select these parents in cotton. The objective of this study was to determine if the the select the se

parental region of origin for cultivars was related to midparent and useful heterosis. We also explored the use of molecular markers (RFLPs) and coefficient of parentage in identifying heterotic effects.

MATERIALS AND METHODS

A half-diallel genetic design consisting of 15 cultivars and one strain, PD 6179, and their 120 F_2 populations were grown at three Mississippi Delta locations in 1990. Soil types over locations were a Beulah fine sandy loam (a coarse-loamy, silt loam, fine-silty, mixed, thermic Typic Hapludalf), Dubbs silt loam (a fine-silty, mixed, thermic Typic Hapludalf) near Stoneville, and Commerce silt loam

(a fine-silty, mixed, nonacid, thermic Aeric Fluvaquent) near Scott, MS. A fourth location was lost due to flooding. Planting dates were 8 May, 7 May, and 30 April, respectively, at the three sites. The 16 genotypes listed in Table 1 originated from the four major cotton growing regions of the United States-four each from the West, Plains, Delta, and East. These 16 entries constituted more than 50% of U.S. plantings in 1990 and 1991 (USDA, AMS, 1991, 1992). The experimental design was a randomized complete-block with four replications. Standard cultural methods for the Mississippi Delta were used. The 136 genotypes were grown in onerow plots; rows were 1.02 by 5.02 m at Stoneville and 0.97 by 5.47 m at Scott. Seeding rate was 18 seed m⁻¹ of row. Fifty boll samples were handharvested from each replication. The samples from the first two replications and from the last two replications were combined to form two 100-boll samples from which yield components were determined and lint obtained for fiber quality

Table 1. Mean lint yield, yield components, and fiber properties of 16 parents from four regions of the United States and means by region for their 120 F₂ populations.

				Yield	l compor	ients	Fiber properties				
		Lint yield		Lint	Boll	Seed	Span length		Span length		Micronaire
Regions	Parents	Total	1 st harv.		wt.	wt.	50%	2.5%	50%	2.5%	
		kg	g ha ⁻¹	%	g	5	m	m	kmNkg ⁻¹	%	units
West	Prema	844	509	35.3	5.75	11.9	15.2	30.7	266	7.3	3.67
	Acala 1517-75	880	577	34.6	5.33	11.3	14.8	31.0	225	7.4	3.62
	Acala SJ-2	741	438	34.3	5.77	12.1	14.3	29.4	218	7.3	3.37
	Acala 510	837	534	35.5	5.46	11.6	14.6	29.7	224	6.8	3.87
Plains	Lankart PR-75	937	698	36.6	5.55	11.3	13.8	28.8	197	7.3	3.73
	Tamcot CD3H	974	847	36.1	5.38	10.2	13.6	28.7	188	7.8	3.68
	Paymaster 145	1024	874	33.4	5.34	11.2	13.8	28.2	193	7.4	3.73
	Paymaster HS-26	912	659	35.6	5.83	12.1	13.8	28.2	210	8.3	4.18
Delta	Delcot 344	1031	705	34.7	4.94	10.5	14.0	30.0	204	7.5	3.92
	Stoneville 453	1138	704	36.4	4.99	11.2	14.5	30.1	195	7.6	3.97
	DES 119	1218	808	34.4	4.81	10.0	14.1	29.9	198	8.0	3.80
	Deltapine 50	1157	844	33.7	4.98	9.9	14.0	29.9	192	8.8	3.90
East	Coker 310	1007	648	36.1	4.79	10.6	14.6	30.4	207	7.3	3.75
	Coker 139	1076	658	37.6	5.07	11.0	14.4	30.6	200	7.4	3.62
	PD 6179	806	584	37.0	5.10	10.9	14.5	30.4	213	7.3	3.37
	McNair 235	1030	752	34.4	4.91	10.7	14.2	29.7	201	7.5	3.68
LSD (0.05)		129	97	1.0	0.32	0.6	0.5	0.7	11	0.6	0.32
F ₂ populations											
West	•	825	514	34.9	5.58	11.7	14.7	30.2	233	7.2	3.63
Plains		962	661	35.4	5.53	11.2	13.8	28.5	197	7.7	3.83
Delta		1136	765	34.8	4.93	10.4	14.2	30.0	197	8.0	3.90
East		980	770	36.3	4.97	10.8	14.4	30.3	205	7.4	3.61
LSD (0.05)		64	49	0.5	0.16	0.3	0.3	0.4	6	0.3	0.16
Parents		976	678	35.4	5.25	11.0	14.3	29.8	208	7.6	3.74
F ₂ populations	:	1066**	748**	35.9**	5.55**	11.1	14.4**	29.8	208	7.5	3.76

*,** Significant at the 0.05 and 0.01 probability levels, respectively, using the error mean square from Table 2.

determinations. The yield components were lint percentage, boll weight, and seed weight. All plots were harvested twice by hand, and lint yields were determined as seedcotton weight per plot times lint percentage. First harvest yields were determined in the first week of September when about 70% of the bolls were mature. Span length (50 and 2.5%), fiber strength (T_1), elongation (E_1), and micronaire were determined from all tests. Combining ability analyses were made using only the F_2 populations (Method four, fixed effects model; Griffing, 1956).

The 16 parents were assayed with 203 random RFLPs. Construction of a cDNA library and the RFLP analyses were accomplished by Biogenetic Services, Brookings, SD. The cDNA library used in the RFLP analysis was constructed using leaf material from six Upland cotton cultivars coming from the four regions. These analyses were conducted using bulk samples of leaf tissue from about 30 plants of each parent. Either EcoRI or EcoRV restriction enzymes were used in the digest of the sample DNA. Fragments were scored as present or absent with their corresponding size in kilobases. More detail on probe construction and RFLP development is reported by Shappley et al. (1996). The genetic distance between parents was determined by the method in Roger (1972).

RESULTS AND DISCUSSION

Mean yield, yield components, and fiber properties for the 16 parents are given in Table 1.

Significant differences were detected for all characteristics. The parental differences due to region of origin are typical of those generally observed in Mississippi Delta cultivar evaluations. As expected, entries originating from the Delta produced the highest yields (1136 kg ha⁻¹) and the Western entries averaged the lowest (825 kg ha⁻¹). The West and Plains cultivars produced the largest bolls and seed. The Western Acalas produced the strongest lint.

Unless otherwise stated, the term heterosis will denote midparent heterosis (comparison of F_2 vs. parental mean). The F-test comparison of F_2 vs. parents in Table 2 shows significant heterosis for five of the 10 characteristics. The highest heterosis was recorded for total and first harvest yield at 90 and 70 kg ha⁻¹, or 9.2 and 10.3%, respectively. Meredith's (1984) summary of 18 states' research on heterosis in cotton reported an average total yield heterosis of 18.5%. Since F2s are expected to exhibit about 50% of the heterosis expressed by the F_1 s, these results closely correspond to that review. Small (but significant) heterosis for lint percentage, boll weight, and 50% span length was also detected, averaging 1.4, 5.7, and 0.7%, respectively. The yield components of lint percentage and boll weight account for 7.2% (1.014 x 1.057) of the 9.2% observed total yield heterosis.

Mean squares for all characters are given in Table 2. The large and significant mean squares for locations and numerous interactions with locations are indicative of large differences in growing

Table 2. Mean squares for lint yield, yield components, and fiber properties.

	df	Lint yield		Yield components			Fiber properties				
Source		Total	1 st harvest	Lint %	Boll wt.	Seed wt.	Span length		Strength		
							50%	2.5%	T ₁	E ₁	Micronaire
							m	m	kNm kg ⁻¹	%	
Locations (L)	2	174869**	86268**	87370**	316**	936**	6915**	785**	4250**	1627**	2776**
Reps.(R)	3	23996**	12834**	2662**	459**	561**	785**	195*	273*	237**	253
Pvs.F ₂	1	17659**	44019**	2179**	740*	24	113**	59	1	24	3
Pvs.F ₂ xL	2	1568**	1017**	98	17	11	108*	44	124	64	8
Parent(P)	15	2769**	2522**	885**	73**	295**	168**	684**	2109**	132**	26**
PxL	30	661**	243	100	21**	33	59**	100*	106	25	5
F ₂	119	1352**	1052**	555**	56**	247**	132**	539**	967**	112**	34**
F,xL	238	445**	302**	97*	11**	39*	39*	81*	75	33**	10*
GCA†	15	2062**	4201**	3182**	344**	1675**	729**	3532**	6757**	616**	184**
SCA‡	104	642**	598**	176**	14**	41**	46**	107**	132**	40**	12**
GCAxL	30	624**	583**	148**	31**	90**	65**	146**	107	24	14**
SCAxL	208	419*	261**	89	8	31	35	72	70	34	9*
Error	405‡	329	188	78	8	30	32	63	91	27	8

*, ** Significant *F*-test at the 0.05 and 0.01 probability levels, respectively, using the error mean square as the divisor; if desired, other *F*-tests can be computed from the data given.

[†] GCA and SCA denote general and specific combining ability, respectively.

‡ Degrees of freedom for error are 1251 for lint yield.

	Diallel of F ₂	populations tha	it involve the f	our parents wi	thin regions		
Source	Df	West	Plains	Delta	East		
GCA†	3	378	311	752*	3142**		
SCA†	2	599	140	333	269		
GCA x L†	6	598	213	64	69		
SCA x L	4	113	510	318	743		
Mean (kg ha ⁻¹)		1048	1019	1181	1074		
% heterosis‡		27.0 **	5.9	4.1	9.6 **		
% Delta parents		92.4	89.9	104.1	94.7		
	Diallel of F	2 populations th	at involve par	ents between t	wo regions		
		West	West	West	Plains	Plains	Delta
Source	df	x Plains	x Delta	x East	x Delta	x East	x East
R1 (Males)(GCA)§	3	1751**	2061**	4987*	1332**	2040**	856*
R2 (Females)(GCA)§	3	1078*	1324**	918*	1145*	1589**	4461**
R1 x R2 (SCA)	9	380	1173**	563	731*	617*	1168**
R1 x L (GCA x L)	6	587	443	405*	1118**	242	128
R2 x L (GCA x L)	6	333	705*	690*	348	269	420
R1 x R2 x L (SCA x L)	18	293	261	243	200	479	519
Mean (kg ha ⁻¹)		1036	1092	1071	1092	1007	1078
f % Heterosis		15.9 **	11.5 **	18.7 **	4.2 **	3.7**	2.0
% Delta parents		91.4	96.3	94.4	96.3	88.8	95.1

Table 3. Total lint yield combining ability analyses mean squares for crosses within and between regions.

*, ** Significant *F*-test at the 0.05 and 0.01 probability levels, respectively, using the error mean square of 329 as the divisor from Table 2 with 1215 degrees of freedom.

† GCA and SCA denotes general and specific combining ability, respectively.

 \ddagger % heterosis is defined as the average over crosses of (F₂ mean) (mean of parents)⁻¹ x 100.

§ R1 (males) indicates the first regional set of parents listed; the second region is coded by R2.

conditions and management. The variation among the 120 F₂s was partitioned into general combining ability and specific combining ability as indicated in Table 2. The general combining ability by location interaction was significant for all traits except bundle strength (T_1) and elongation (E_1) . The specific combining ability by location interaction showed significant effects for total and first harvest yield and for micronaire. Assuming the 16 parents represented a random sample of available parents, the total yield variance components were as follows: 22.5 for specific combining ability by location, 3.7 for general combining ability by location, 18.6 for specific combining ability, and 7.2 for general combining ability. The specific combining ability and specific combining ability by location accounted for 79% [(22.5 + 18.6) (52.0)⁻¹ x 100] of the total genetic variance components. While this test represented a small sample of possible parents and environments, it does indicate that using heterosis in cotton will require extensive testing to determine the best (highest yielding) combination of parents.

Of importance in this study was the search for clues as to methods for selecting the best parents. The correlation between total yield of F_2s and their

midparents was 0.42 (P < 0.01). While this correlation suggests that general parental performance is helpful in choosing parents, the large unexplained F₂ variability also indicates that mean parental performance alone is insufficient to choose parents for high yielding F₂s.

To evaluate whether cultivar region of origin was an important criterion in the expression of heterosis, we partitioned the total yield analysis into subgroups as indicated in Table 3. Significant heterosis among $F_{2}s$ produced from within the West and East regions was detected (Fig. 1). The greatest heterosis was observed in West x West $F_{2}s$ (27.0%). The general trend is for the lower yielding parents to produce the higher heterosis. Parents grown in regions for which they are not adapted have a great potential for dominance gene action to be expressed. Significant heterosis within the East region was due to the low parental average of PD 6179 (806 kg ha⁻¹) and the high F_2 yield of Coker 139 x McNair 235 (1240 kg ha⁻¹).

Significant heterosis was detected for all interregional crosses, except the Delta x East region. Significant specific combining ability was detected among all regions except the West x Plains and West



Fig. 1. Mean F2 and midparent (MP) yield performance for groups of crosses within and between the four major cotton-growing regions of the United States. Within a region, the mean is derived from six crosses; between regions it is calculated from 16 crosses. * , ** Statistical significance at the 0.05 and 0.01 probability levels, respectively, for comparing the F_2 vs. midparents.

x East. The only major trend toward selecting good parents for F_2 performance was that cultivars developed in the Delta had the highest general combining ability. This was expected because three cultivars (DES 119, Stoneville 453, and Deltapine 50) were selected at Stoneville and Scott, the same locations where these evaluations were conducted. As reported in the combining ability study by Calhoun (1997), other good combiners from parents developed outside the Mid-South could be detected if appropriate searches are made.

According to Bowman et al. (1997), the mean coefficient of parentage for the three Delta cultivars is 0.25. A fourth good combiner was Coker 139 from the East region. Its mean coefficient of parentage with those three cultivars was high, 0.32. The fifth good combiner was Delcot 344, which was developed in the North Delta by Sappenfield (1987). Its mean coefficient of parentage with the other four cultivars is 0.20. Unexpectedly, the West cultivars proved to be both good in general and specific combining abilities. The best combiner from the West was 'Prema'. Its mean coefficient of parentage with the previous five cultivars was only 0.03. The average coefficient of parentage for all parents, excluding PD 6179, was 0.09. Strain PD 6179's relationship wasn't available from Bowman et al. (1997).

Table 4. Lint yield and strength (T₁) of the six parents with the highest general combining ability and their 15 F₂s.

Parents and their F ₂ s	Lint yield	T ₁		
	kg ha ⁻¹	kNm kg ⁻¹		
Prema	844	266		
Coker 139	1076	200		
Delcot 344	1031	204		
Stoneville 453 (STV 453)	1138	195		
DES 119	1218	198		
Deltapine 50 (DPL 50)	1157	192		
Prema x Coker 139	1217	212		
x Delcot 344	1133	224		
x STV 453	1065	220		
x DES 119	1160	223		
x DPL 50	1227	220		
Coker 139 x Delcot 344	1012	211		
x STV 453	1123	195		
x DES 119	1178	192		
x DPL 50	1174	185		
Delcot 344 x STV 453	1128	194		
x DES 119	1314	193		
x DPL 50	1137	200		
STV 453 x DES 119	1264	186		
x DPL 50	1087	186		
DES 119 x DPL 50	1158	192		
LSD (0.05)	129	11		

The total yield performance and bundle strength of the six parents with the highest general combining abilities and their 15 F₂s are given in Table 4. The four highest yielding F₂s were Prema x Coker 139, Prema x Deltapine 50, Delcot 344 x DES 119, and Stoneville 453 x DES 119 with yields of 1217, 1227, 1314, and 1264 kg ha⁻¹, respectively. The average yield of these four $F_{2}s$ (1256 kg ha⁻¹) was significantly higher than the average for the four Delta cultivars (1136 kg ha⁻¹). Delcot 344 was also a superior combiner in the studies by Tang et al. (1993). In their studies averaged over four environments, the highest yielding F2 was Delcot 344 x Coker 315, with 1529 kg ha⁻¹. The average of their four regional checks, DES 119, Deltapine 50, Stoneville 453, and Coker 315 was 1277 kg ha⁻¹, significantly less (P < 0.01) than their four $F_{2}s$ produced from crosses with Delcot 344. These F₂s averaged 1428 kg ha⁻¹. Prema crossed with the other five cultivars listed in Table 4, not only produced high yields (an average of 1260 kg ha⁻¹), but also produced F₂s whose average bundle strength was 220 km N kg⁻¹. The average yield of the 10 remaining $F_{2}s$ was 1157 kg ha⁻¹ and their average strength was 196 km N kg⁻¹.

We assayed the 16 parents with 203 random RFLPs and determined pairwise genetic distances (Roger, 1972). The correlation of genetic distance

and midparent heterosis was small, r = 0.08 (Meredith, 1995). The coefficient of parentage was also correlated with heterosis; it, too, was small (r = 0.05) and of no value in selecting parents.

SUMMARY

These results were from a small sample of parents that could be used to detect heterosis patterns. The samples did cover all four major cotton growing regions. The only trend that evolved was that the parents with better general combining ability, were those that were bred and developed in the Delta. This suggests that at least one parent should be a well-adapted genotype. One good combiner came from the North Delta (Delcot 344), one came from the East (Coker 139), and one came from the West (Prema), indicating that choosing the second parent is a bit more difficult. No pattern of regional source for the second parent was evident. An exception exists when fiber quality is a major breeding objective. Then, one must choose at least one parent that has above average fiber properties. We tried to correlate genetic distance and coefficient of parentage with heterosis, but this effort also showed no significant associations. While genetic differences among potential parents are required to obtain high heterosis, it is no assurance that diverse parents will produce high heterosis. Furthermore, genetic distance estimated from pedigree analysis or with molecular markers appeared inadequate for identifying those genetic differences among parents that are important for heterosis. The encouraging aspect of this study was that good combiners were detected from a small sample of parents. None of these parents were selected for this study based on their known combining ability. One could speculate that larger parental tests, say several hundred, would lead to even greater expressions of useful heterosis.

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