Heterotic Effects in Topcrosses of Modern and Obsolete Cotton Cultivars

B. T. Campbell,* D. T. Bowman, and D. B. Weaver

ABSTRACT

Historically, reselection, pedigree, and mass-selection breeding methods have been used to develop open-pollinated cultivars of upland cotton (*Gossypium hirsutum* L.). As a result, modern cotton cultivars should have accumulated additive genetic effects with time, while also possessing fewer nonadditive gene effects than obsolete cultivars. A topcross test was conducted to compare the heterotic effects of obsolete and modern cultivars for yield, yield components, and fiber quality. Significant differences were detected between heterosis values for the modern and obsolete cultivar groups for seed cotton yield, lint yield, lint percentage, and boll weight. No significant heterotic effects were detected for fiber quality. The obsolete group of cultivars showed average lint yield heterosis values of 34% compared with 23% for the modern cultivars. Both cultivar groups displayed significant, but similar heterosis values for the number of bolls per square meter (17 and 15%, respectively). The major yield component associated with lint yield heterosis for both groups was bolls per square meter, although boll weight heterosis also contributed to lint yield heterosis for the obsolete cultivars. Although modern cultivars produced considerable heterotic effects for yield, this study demonstrates that obsolete cultivars may provide an additional source of nonadditive genetic effects that can be exploited in a hybrid production system.

B.T. Campbell, USDA-ARS, Coastal Plains Soil, Water, and Plant Research Center, 2611 W. Lucas St., Florence, SC 29501; D.T. Bowman, Dep. of Crop Science, North Carolina State Univ., Raleigh, NC 28796; and D.B. Weaver, Dep. of Agronomy and Soils, Auburn Univ., Auburn, AL 36849. Received 26 June 2007. *Corresponding author (todd.campbell@ars.usda.gov).

Capitalizing on the effects of hybrid vigor or heterosis presents an intriguing opportunity to increase the yield of upland cotton (*Gossypium hirsutum* L.). During the last 50 yr, studies have been conducted to explore the effects of heterosis using both F_1 and F_2 hybrids. Most of these studies, involving the effects of heterosis for yield and its components, have been summarized for cotton by Meredith (1984). A more recent summary by Meredith (1990) reported that yield heterosis values averaged 21.4 and 10.7% for F_1 and F_2 hybrids, respectively. In addition, several studies have reported that heterosis for yield component traits contribute to the heterosis for yield. The majority of studies have reported that boll weight and the number of bolls per unit area contribute a large portion to yield heterosis (White and Richmond, 1963; Miller and Lee, 1964; White and Kohel, 1964; Marani, 1968; Al-Rawi and Kohel, 1969; Meredith and Bridge, 1972; Tang et al., 1993a). Lee et al. (1967) also reported the influence of lint percentage heterosis on the overall yield heterosis. Yet, studies investigating heterosis for fiber quality traits do not report large heterosis values overall (Meredith, 1990; Tang et al., 1993b).

To date, the successful commercialization of hybrid cotton has been realized outside of the United States. To our knowledge, Hazera Seeds Inc. (Coconut Creek, FL), a subsidiary of Hazera Genetics Inc. (Israel), is the only company marketing commercial hybrid

Published in Crop Sci. 48:593–600 (2008).
doi: 10.2135/cropsci2007.06.0362

cotton seed in the United States. These hybrids are targeted for the U.S. pima (*G. barbadense* L.) production area of California and are interspecific hybrids between *G. hirsutum* and *G. barbadense* (www.hazerainc.com/hsi, verified 11 Jan. 2008). Outside of the United States, however, China and India have rapidly adopted hybrid cotton production systems and increased yield. According to Dongre and Parkhi (2005), hybrid cotton in India represents approximately 45% of the total production area and accounts for about 55% of India's cotton production. Dong et al. (2006) reported that hybrid cotton production in China since 2000 covers approximately 20% of the total acreage. In addition, Dong et al. (2004) reported that hybrid Bt cotton in India has increased yield 20% compared with pure-line Bt cotton cultivars. In the United States, hybrid upland cotton production has not successfully emerged to date.

Meredith and Brown (1998) reported that the major limiting factor preventing U.S. hybrid cotton production and the use of heterosis is the lack of an efficient and dependable system for producing F_1 or F_2 hybrid seed. This limiting factor still exists today. In the 1990s, however, the U.S. cotton industry began marketing F_2 seed for commercialization following reports by Meredith and Bridge (1972) and Olvey (1986) indicating the feasibility of F_2 hybrids. Unfortunately, the commercialization of F_2 hybrid seed in the United States did not prove to be a success, mainly due to the ineffectiveness of the male gametocide, TD-1123 (Meredith and Brown, 1998).

Nonetheless, the prospect of commercializing heterosis for U.S. cotton production continues to be appealing today because of success in China and India and well-known heterotic effects for yield. In the 1990s, the breeding approach used to capture yield heterosis was based on choosing the highest yielding and most productive parents to develop hybrid seed. Davis (1978) stated that the highest yielding hybrids usually result from crosses involving the highest yielding cultivars. Selecting parental lines to produce hybrids in this way would indicate the ability to accumulate additive genetic effects. As such, studies have demonstrated a close relationship between parental performance and that of their hybrids (Miller and Lee, 1964; Wu et al., 2004). Meredith and Brown (1998) reported, however, that unexplained variability, due primarily to nonadditive genetic effects, would hinder choosing hybrid parents based on parental performance alone and suggested selecting parents based on their known combining ability.

Combining ability has been investigated in cotton for specific crosses in numerous studies during the last 50 yr. These studies demonstrate the importance of selecting parental lines based on their individual combining ability to maximize the probability of successful genetic improvement. Overall, these studies were performed to determine the nature of gene action for specific traits within specific populations. The nature of gene action is important to consider, because heterosis is due to the accumulation of nonadditive genetic effects that can result from dominance, partial dominance, overdominance, or epistasis. Young and Murray (1966), Marani (1968), Al-Rawi and Kohel (1969), Meredith and Bridge (1972), and Tang et al. (1993a) reported that dominance was the predominant form of gene action responsible for yield and yield component heterosis in F_1 hybrids. Several studies also reported the presence of epistatic gene effects on heterosis expression (Lee et al., 1967; Al-Rawi and Kohel, 1969; Meredith and Bridge, 1972; Meredith, 1990), while other studies comparing F_1, F_2, and F_3 hybrids reported the predominance of nonadditive effects in F_1 hybrids followed by increased additive genetic effects in F_2 and F_3 hybrids (Meredith and Bridge, 1973; Tang et al., 1993a). The cumulative results of these studies prompted cotton breeders to concentrate efforts to accumulate additive genetic effects for genetic improvement until the development of a feasible hybrid seed production system (Lee et al., 1967; Meredith and Bridge, 1972).

Subsequently, cotton breeders have been selecting cultivars from open-pollinated populations since the early 1900s, primarily using reselection, pedigree, and mass selection (Calhoun et al., 2006). These breeding schemes have accumulated additive gene effects and may have inadvertently reduced nonadditive gene effects that have contributed to a decline in yield heterosis. If this were true, the breeder wishing to utilize heterosis might attempt to incorporate nonadditive gene effects from obsolete lines into more agronomically desirable parents. Several studies have compared the mean performance of modern and obsolete cultivars with the objective of determining the rate of genetic gain for yield with time (Bridge et al., 1971; Bridge and Meredith, 1983; Culp, 1984). These studies demonstrated that modern cultivars produce higher yields primarily by increasing lint percentage and bolls per square meter while reducing boll weight (Bridge et al., 1971; Bridge and Meredith, 1983; Culp, 1984). In addition, a series of studies demonstrated that modern cultivars produce higher yields due to their ability to transition into reproductive growth earlier in the growing season and to partition more dry matter resources into reproductive structures (Wells and Meredith, 1984a,b,c). To our knowledge, there are no reports directly comparing the heterotic effects of obsolete and modern cotton cultivars. White and Richmond (1963) studied heterosis among crosses of primitive, foreign, and cultivated cottons and found only two instances of heterosis for yield, both involving an old Cambodian type.

The objective of this study was to compare the effects of heterosis resulting from crosses involving several obsolete, ancestral cultivars and crosses resulting from several modern cultivars. We hypothesize that more nonadditive gene effects exist in crosses involving obsolete cotton cultivars than modern cotton cultivars.

MATERIALS AND METHODS

Plant Materials and Cultivar Descriptions

In a preliminary study in 1995, Georgia King, a modern cultivar, was topcrossed with five modern cultivars (Carolina ES-300, Deltapine 50, Deltapine 90, DES 119, and S-35) and 10 obsolete cultivars (Acala 5675, Delfos, Half and Half, Hopi Moencopi, Kekchi, Lightning Express, Lone Star, Rowden, Trice, and Wannamaker's Cleveland) to produce F_1 seed. Georgia King was released in 1990 and derived from a cross between 'Tifcot 56' and 'McNair 235'. Carolina ES-300 is a blend of Coker cultivars, e.g., Coker 310, Coker 312, etc., and was released in 1992. Deltapine 50 was released in 1984 and Deltapine 90 in 1981; DES 119 was made available in 1985 and S-35 in 1989. The choice of Georgia King as the topcross tester was arbitrary.

Acala 5675, a reselection of 'Acala 5', was released in 1941; Acala 5 dates back to 1917 (Calhoun et al., 2006). A series of Delfos cultivars, which were reselections from 'Foster', were offered beginning in 1920. Half and Half was released in 1905 as a reselection of 'Cook Improved'. Hopi Moencopi was an ancient cultivar of the Hopi Indians of Arizona and was collected in the early 1930s. Kekchi was introduced from Mexico in 1904. Lightning Express was a reselection of 'Express 350' released in 1923. Lone Star was a reselection of 'Jackson Round Boll' released in 1905. Trice was also released in 1905 as a reselection of 'Tennessee Green Seed'. Rowden was a reselection of 'Bohemian' released in 1900. Wannamaker's Cleveland was released in 1915 as a reselection of 'Cleveland'.

A second set of topcrosses was made in 2005 with the same topcross tester Georgia King. All F_1 hybrid seed was produced by hand emasculation and hybridization during the summer of 2005 in North Carolina, South Carolina, and Alabama. In this set of topcrosses, five modern cultivars were used and included Deltapine 51, Deltapine 90, Delta Pearl, FiberMax 966, and SureGrow 747. In addition, five obsolete cultivars were used and included Half and Half, Hopi Moencopi, Lone Star, Rowden, and Young's Acala. Deltapine 51 is a reselection of Deltapine 50, which was used in the preliminary study. Delta Pearl resulted from a cross of 'Deltapine 5816' and 'Sicala 34'. SureGrow 747 has 87.5% DES 119 in its pedigree, which was used in the preliminary study. FiberMax 966 was developed in Australia and made commercially available in the United States in 2000. Young's Acala is an accession from Mexico introduced into upland cotton breeding programs in the early 1900s as a potential source of boll weevil (*Anthonomus grandis* Boheman) resistance.

Field Trials

In a preliminary study, a field trial was conducted in 1995 at the Central Crops Research Station near Clayton, NC. The trial included two replicates of 31 entries each evaluated in two-row plots, 11.1 m long. Row width was approximately 1 m. Field plots were arranged with each F_1 hybrid paired between its respective parents and these sets, randomized within blocks. The trial was planted 5 May and harvested 26 October. Fertilization, weed control, insect control, and defoliation measures were managed following established local practices. Plant growth regulators were not used.

Agronomic data were collected on plant height, boll weight, lint yield, lint percentage, bolls per square meter, date of first flower, and earliness as measured by the percentage of bolls open 2 wk before harvest. Fiber quality data for fiber length, strength, micronaire, and uniformity index were measured using high-volume instrumentation analyses. A 25-boll sample was collected before harvest to determine lint percentage, boll weight, and fiber properties.

In 2006, a set of three field trials was conducted in Auburn, AL, Florence, SC, and Rocky Mount, NC. Each of the three trials was designed and conducted in much the same manner as the 1995 study and incorporated a randomized complete block design that included four replicates of the 10 F_1 hybrids and 11 parental lines. Similar to 1995, data collected included the agronomic traits seed yield, lint percentage, lint yield, boll weight, and bolls per square meter. No data were collected on plant height and earliness. High-volume instrumentation fiber quality data were collected for the fiber properties length, strength, uniformity index, elongation, micronaire, and short fiber content.

Data Analysis

In the 1995 trial, heterotic effects were calculated for each trait and entry by subtracting midparent values from F_1 values in each replicate. The midparent value was calculated as the mean of Georgia King and each F_1's respective parent. For each trait, heterosis percentage was determined by dividing heterotic effects by the midparent values and multiplying by 100. Heterosis percentage values were subjected to analysis of variance by PROC GLM to test if differences existed between modern and obsolete cultivars for each agronomic and fiber quality trait (SAS Institute, 2002).

In the 2006 trials, entry means for each trait were calculated in each of the three environments. Mean data were used to calculate the midparent, heterotic effects, and heterosis percentage values for each of the five modern and five obsolete cultivars. Mean trait data and heterosis percentage values were subjected to analysis of variance by PROC GLM using the following model:

$$Y_{ijk} = \mu + l_i + g_j + c_{k(j)} + \varepsilon_{ijk}$$

where Y_{ijk} is the mean value of the ith location of the jth group of the kth entry, μ is the overall mean, l_i is the effect of the ith location, g_j is the effect of the jth group, $c_{k(j)}$ is the effect of the kth entry in the jth group and ε_{ijk} is the random error. The ε_{ijk} values are assumed to be independently distributed with constant variance. The LSD for each trait was calculated among all parents (including the tester Georgia King), the 10 F_1 hybrid combinations, the 10 midparent values, and the 10 heterosis values. The LSD allowed individual entry comparisons for each trait.

Coefficients of parentage between and among the tester (Georgia King) and each cultivar (obsolete and modern) included in the 1995 and 2006 trials were calculated as published by Bowman et al. (1997). Coefficients for cultivars included in the 2006 trials are provided in Table 1. For each set of cultivars included in the 1995 and 2006 trials, Pearson correlations were calculated to examine the relationship between genetic distance from the tester as estimated by coefficients of parentage and heterosis for each trait, with significant differences within the modern or obsolete cultivar groups.

RESULTS AND DISCUSSION

Modern Cultivars

Even though mass selection, reselection, and recurrent selection via pedigree breeding have been predominant breeding schemes, sufficient nonadditive genetic effects exist in the modern cultivars for several agronomic traits (Table 2). In the 2006 trials, the largest mean heterosis values for modern cultivars were identified for seed cotton yield (23%), lint yield (23%), and bolls per square meter (15%). FiberMax 966 showed the highest amount of heterosis for lint yield (39%) compared with the other modern cultivars included in this study, while SureGrow 747 produced the lowest amount of heterosis for lint yield (14%). Similarly, in the 1995 trial, the mean heterosis values for lint yield and bolls per square meter were 19 and 15%, respectively (data not shown). Miller and Lee (1964) also found a midparent heterotic effect for lint yield of 18% for 22 sets of topcrosses and 20% for a subset of nine topcrosses.

In terms of fiber quality traits, the 2006 trials showed relatively little heterosis for the fiber traits measured in this study (Table 3). The mean heterosis values for modern cultivars were all fairly close to 0%, with positive heterosis values for length, micronaire, and short fiber content and negative heterosis values for strength, elongation, and uniformity index. Data from the 1995 trial also showed relatively little heterosis for fiber traits (data not shown).

Obsolete Cultivars

In the 2006 trials, the five obsolete cultivars produced large heterosis values for seed cotton yield (31%), lint yield (34%), boll weight (12%), and bolls per square meter (17%) (Table 2). Half and Half and Lone Star produced the highest heterosis values for lint yield at 43 and 39%, respectively. Young's Acala produced the lowest heterosis value for lint yield at 25%. In the 1995 trial, the mean of the 10 obsolete cultivars also produced large heterosis values of 34% for lint yield and 33% for bolls per square meter (data not shown). In the 1995 trial, Acala 5675 had a heterosis value of 32% for lint yield. Acala 5675 was also in the study by Miller and Lee (1964), but only displayed heterosis values of 8 and 6% in their study, which used 'Coker 100A' as the tester.

In terms of fiber quality traits, the 2006 trials showed relatively little heterosis for the fiber traits measured in this study (Table 3). The mean heterosis values for obsolete cultivars were all fairly close to 0%, with positive heterosis values for length and strength and negative heterosis values for elongation, micronaire, and short fiber content. The mean heterosis value for uniformity was 0%. Similarly, data from the 1995 trial also showed relatively little heterosis for fiber traits (data not shown).

Modern vs. Obsolete Cultivars

Results of analysis of variance for agronomic and fiber quality trait heterosis values for the 2006 trials are presented in Tables 4 and 5. Before conducting the analysis of variance for agronomic and fiber quality trait heterosis values presented in Tables 4 and 5, location-by-group interaction effects were tested and found nonsignificant for each trait measured. Subsequently, Tables 4 and 5 provide statistical tests considering only main effects, thereby providing a more conservative statistical test. For the agronomic traits, significant differences among cultivars within a group (modern or obsolete) were detected for lint yield and lint percentage. Significant differences were also detected between the modern and obsolete groups of cultivars for seed cotton yield, lint yield, lint percentage, and boll weight. No significant differences were detected between groups for bolls per square meter. Results from the 1995 trial showed heterosis differences between modern and obsolete cultivars for lint yield, lint percentage, and bolls per square meter. The results from the 2006 and 1995 trials are consistent with similar topcross and diallel

Table 1. Relationship (coefficient of parentage) between and among the tester (Georgia King) and all parents in the 2006 topcross study.

Parent	Modern					Obsolete				
	Deltapine 90	SureGrow 747	Deltapine 51	Delta Pearl	FiberMax 966	Hopi Moencopi	Rowden	Lone Star	Young's Acala	Half and Half
Georgia King	0.057	0.112	0.090	0.036	0.031	0.017	0.061	0.072	0.022	0.035
Deltapine 90		0.114	0.151	0.517	0.259	0	0.071	0.063	0.084	0.010
SureGrow 747			0.445	0.066	0.042	0.009	0.071	0.094	0.014	0.028
Deltapine 51				0.086	0.046	0.007	0.071	0.076	0.011	0.008
Delta Pearl					0.152	0.008	0.040	0.036	0.049	0.007
FiberMax 966						0.002	0.023	0.026	0.031	0.040
Hopi Moencopi							0	0	0	0
Rowden								0.422	0	0
Lone Star									0	0
Young's Acala										0

Table 2. Parental (P), F_1, midparent (MP), and heterosis (Het) values for agronomic traits involving topcrosses of five modern and five obsolete cotton cultivars combined in Alabama, North Carolina, and South Carolina in 2006.

Parent	Seed cotton yield			
	P	F1	MP	Het
	— kg ha^{-1} —			%
Delta Pearl	2518	2652	2249	17
Deltapine 51	2030	2445	2005	23
Deltapine 90	2547	2646	2264	17
FiberMax 966	2290	2941	2135	38
SureGrow 747	2152	2468	2066	18
Half and Half	930	2015	1455	38
Hopi Moencopi	1308	2166	1644	31
Lone Star	1358	2302	1669	38
Rowden	1273	1990	1627	23
Young's Acala	1495	2199	1738	26
Georgia King (tester)	1980	–	–	–
LSD (0.05)	491	313	257	13
P > *F*	0.0001	0.0008	0.0001	0.0386

Parent	Boll weight			
	P	F1	MP	Het
	— g —			%
Delta Pearl	5.2	5.9	5.4	9.6
Deltapine 51	5.2	5.7	5.4	5.9
Deltapine 90	5.3	5.7	5.4	4.9
FiberMax 966	5.9	6.3	5.8	9.4
SureGrow 747	5.6	5.8	5.6	2.5
Half and Half	5.4	6.3	5.5	15.0
Hopi Moencopi	6.1	6.6	5.9	12.7
Lone Star	6.0	6.6	5.8	14.3
Rowden	4.7	5.6	5.2	8.8
Young's Acala	6.0	6.4	5.8	10.3
Georgia King (tester)	5.6	–	–	–
LSD (0.05)	0.7	0.3	0.4	8.4
P > *F*	0.0670	<0.0001	0.0746	0.2544

Parent	Lint yield			
	P	F1	MP	Het
	— kg ha^{-1} —			— % —
Delta Pearl	1007	1081	901	19
Deltapine 51	775	969	785	24
Deltapine 90	989	1054	892	18
FiberMax 966	936	1201	865	39
SureGrow 747	911	990	853	14
Half and Half	371	838	583	43
Hopi Moencopi	373	754	584	29
Lone Star	453	868	624	39
Rowden	296	719	545	32
Young's Acala	510	814	652	25
Georgia King (tester)	794	–	–	–
LSD (0.05)	199	151	257	13
P > *F*	<0.0001	0.0004	<0.0001	0.0135

Parent	Bolls per square meter			
	P	F1	MP	Het
	— no. m^{-2} —			%
Delta Pearl	54.3	50.4	47.0	6.4
Deltapine 51	43.1	47.9	41.4	15.9
Deltapine 90	54.2	52.0	47.0	11.0
FiberMax 966	43.1	52.3	41.4	26.2
SureGrow 747	42.8	48.3	41.2	16.0
Half and Half	20.1	36.0	32.4	20.5
Hopi Moencopi	25.2	37.4	32.6	14.6
Lone Star	25.4	39.3	35.1	20.6
Rowden	30.5	39.9	34.0	15.6
Young's Acala	28.2	38.8	32.8	13.9
Georgia King (tester)	39.7	–	–	–
LSD (0.05)	9.2	6.1	4.6	13.4
P > *F*	<0.0001	0.0003	<0.0001	0.4705

Parent	Lint percentage			
	P	F1	MP	Het
Delta Pearl	39.8	40.7	39.9	1.9
Deltapine 51	37.9	39.5	38.9	1.5
Deltapine 90	38.8	39.8	39.4	1.0
FiberMax 966	40.8	40.9	40.4	1.2
SureGrow 747	42.0	39.7	41.0	–3.3
Half and Half	39.8	41.6	39.9	4.1
Hopi Moencopi	28.6	34.8	34.3	1.4
Lone Star	33.4	37.7	36.7	2.8
Rowden	23.0	36.2	31.5	14.9
Young's Acala	34.1	37.1	37.1	0.2
Georgia King (tester)	40.0	–	–	–
LSD (0.05)	1.7	1.6	0.9	4.1
P > *F*	<0.0001	<0.0001	<0.0001	0.0001

studies previously reporting significant heterosis for yield, boll weight, and bolls per square meter (White and Richmond, 1963; Miller and Lee, 1964; White and Kohel, 1964; Marani, 1968; Al-Rawi and Kohel, 1969; Meredith and Bridge, 1972; Tang et al., 1993a).

Although lint yield heterosis was identified in both modern and obsolete progeny, data revealed that hybrids from obsolete parents approached the modern F_1s in yielding ability. On average, obsolete cultivars yielded 57% lower than modern cultivars, while obsolete hybrids yielded only 25% lower than modern hybrids. In addition, the obsolete group of cultivars displayed heterosis for lint percentage (4.7%), while the modern group showed negligible heterosis (0.4%). Obsolete cultivars displayed almost twice the boll weight heterosis of the modern cultivars. Similarly, both groups of cultivars produced significant heterosis for bolls per square meter. Correlations between heterosis values for lint yield and its component traits revealed that most of the increased lint yield heterosis for obsolete ($r = 0.76$, $P < 0.01$) and modern cultivars ($r = 0.90$, $P < 0.01$) was associated with heterosis for bolls per square meter. However, boll weight heterosis also contributed to the lint yield heterosis for obsolete cultivars ($r = 0.63$) at $P < 0.01$. Boll weight and lint yield heteroses were not associated in the modern cultivars. These results are consistent with previous studies suggesting a relationship between boll weight, bolls per square meter, and lint yield (White and Richmond, 1963; Miller and Lee, 1964; White and Kohel, 1964; Marani, 1968; Al-Rawi and Kohel, 1969; Meredith and Bridge, 1972; Tang et al., 1993a). The nonassociation of boll weight and lint yield heteroses in the modern cultivars is probably related to the modern cultivars possessing lower boll weights. Reports have indicated that modern cultivars express increased yield potential by producing a greater number of smaller sized bolls per unit area (Bridge et al., 1971; Bridge and Meredith, 1983).

For the fiber quality traits, differences were detected among cultivars within a group (modern or obsolete) for length and uniformity index only. No significant differences were detected between the modern and obsolete groups of cultivars for any of the fiber quality traits measured. In general, these data suggest that negligible nonadditive genetic effects are present in topcross progeny derived from either modern or obsolete cultivars. Hence, improved fiber quality derived from the modern and obsolete cultivars used in this study would require the accumulation of additive genetic effects in the resulting progeny. These results are consistent with previous reports identifying negligible heterotic effects for fiber quality (Meredith, 1990; Tang et al., 1993b).

Collectively, these data suggest that substantial nonadditive genetic variance remains in modern and obsolete upland cotton cultivars for agronomic traits and thus would confirm their desirability as parents. It is important to note that this study also provides evidence that beneficial nonadditive genetic effects for lint yield can be accumulated without negatively impacting fiber quality. Data from this study also suggest that additional nonadditive genetic effects may be gleaned from obsolete cultivars for lint yield and other agronomic traits. Hence, obsolete cultivars may present a useful source for capturing yield

Table 3. Parental (P), F_1, midparent (MP), and heterosis (Het) values for fiber quality traits involving topcrosses of five modern and five obsolete cultivars combined in Alabama, North Carolina, and South Carolina in 2006.

Parent	Length				Strength				Elongation			
	P	F_1	MP	Het	P	F_1	MP	Het	P	F_1	MP	Het
	mm			%	kN m kg^{-1}				%			
Delta Pearl	29.4	28.7	28.7	0.2	318.2	318.8	315.7	1.0	4.4	4.4	4.6	–5.4
Deltapine 51	28.4	28.3	28.1	0.5	290.9	302.2	302.0	0.1	5.5	5.3	5.2	1.7
Deltapine 90	28.0	28.0	28.0	0.2	327.4	307.7	320.2	–3.8	4.8	4.6	4.9	–5.5
FiberMax 966	28.4	28.7	28.2	1.9	321.7	324.3	317.4	2.1	4.0	4.3	4.5	–5.3
SureGrow 747	28.2	27.9	28.0	–0.5	287.0	290.9	300.1	–3.0	6.2	5.3	5.6	–4.8
Half and Half	22.7	25.0	25.3	–1.1	268.9	266.8	291.0	–8.2	5.8	5.4	5.4	1.5
Hopi Moencopi	30.4	29.9	29.2	2.6	297.4	313.7	305.2	2.8	4.9	4.9	4.9	0.1
Lone Star	29.2	28.7	28.5	0.8	285.6	297.2	299.4	–0.7	5.8	5.4	5.4	1.5
Rowden	25.3	27.4	26.6	2.9	246.2	290.0	279.7	3.7	6.8	5.3	5.9	–9.9
Young's Acala	26.7	27.7	27.3	1.5	298.1	316.4	305.6	3.4	4.3	4.5	4.6	–3.5
Georgia King (tester)	27.9	–	–	–	313.1	–	–	–	5.0	–	–	–
LSD (0.05)	1.1	0.8	0.6	2.8	14.4	10.7	7.2	4.2	0.6	0.3	0.3	7.0
$P > F$	<0.0001	<0.0001	<0.0001	0.3214	<0.0001	<0.0001	<0.0001	0.0019	<0.0001	<0.0001	<0.0001	0.1150

Parent	Uniformity index				Micronaire				Short fiber content			
	P	F_1	MP	Het	P	F_1	MP	Het	P	F_1	MP	Het
	%								%			
Delta Pearl	83.3	82.9	83.2	–0.5	5.3	5.3	5.2	2.6	8.2	8.2	8.1	1.3
Deltapine 51	83.6	82.9	83.4	–0.5	5.2	5.3	5.2	2.5	8.5	8.5	8.3	2.2
Deltapine 90	82.6	82.5	82.9	–0.5	5.3	5.2	5.2	0.1	8.5	8.7	8.3	4.7
FiberMax 966	82.6	82.5	82.9	–0.5	5.3	5.3	5.2	0.8	8.3	8.4	8.2	3.4
SureGrow 747	83.8	82.9	83.5	–0.7	5.5	5.5	5.3	3.8	8.1	8.5	8.1	5.0
Half and Half	78.9	80.8	81.0	–0.3	4.9	5.2	5.0	3.0	12.8	9.8	10.4	–6.8
Hopi Moencopi	83.6	83.5	83.4	0.2	3.8	4.6	4.5	2.9	8.1	7.9	8.1	–1.8
Lone Star	83.1	82.9	83.1	–0.2	3.8	4.5	4.5	0.6	8.3	8.4	8.2	3.5
Rowden	81.9	83.0	82.5	0.5	5.8	5.0	5.4	–8.8	8.6	8.2	8.3	–1.0
Young's Acala	82.3	82.4	82.7	–0.4	4.4	4.9	4.8	2.0	8.9	8.5	8.5	0.6
Georgia King (tester)	83.2	–	–	–	5.1	–	–	–	8.1	–	–	–
LSD (0.05)	0.7	0.9	0.4	1.2	0.3	0.3	0.1	5.5	0.8	0.9	0.4	9.2
$P > F$	<0.0001	0.0053	<0.0001	0.8325	<0.0001	0.0010	<0.0001	0.0386	<0.0001	0.1831	<0.0001	0.5441

heterosis if the objective of the program is to market F_1 or F_2 hybrid seed.

Relationship between Genetic Distance and Heterosis

To explore the ability of genetic distance to predict heterotic effects, correlations were calculated for traits exhibiting significant heterotic differences within a cultivar group. Traits included in this analysis included lint yield, lint percentage, fiber length, and uniformity index. For each cultivar within a group (modern or obsolete), the correlation between genetic distance (from the tester, Georgia King) and heterosis was not significant for any of these traits in the 1995 or 2006 trials. These data indicate that increased genetic distance, as measured by coefficient of parentage, is not a good predictor of heterosis for the traits measured. Our findings are similar to those reported by Meredith and Brown (1998) in their attempt to correlate heterosis and genetic distance using both coefficient of parentage and molecular marker based calculations of genetic distance.

Table 4. Analysis of variance for agronomic trait heterosis values (calculated as the heterotic effect divided by the midparent value multiplied by 100) of two groups of topcrosses consisting of five obsolete and five modern cotton cultivars grown in Alabama, North Carolina, and South Carolina in 2006.

Source of variation	df	Mean square				
		Seed cotton yield	Lint yield	Lint percentage	Boll weight	Bolls per square meter
Location	2	263.66	105.04	35.50*	11.95	139.93
Group	1	581.16*	855.86**	134.23**	250.35*	27.96
Entries(Group)	8	186.76	231.43*	58.63**	24.48	97.95
Error	18	87.66	89.20	8.38	35.12	89.68
Mean heterosis obsoletes, %		31	34	4.7	12.2	17.0
Mean heterosis moderns, %		23	23	0.4	6.5	15.1

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

CONCLUSIONS

The long history of heterosis research in cotton provides definitive evidence that hybrid cotton production will indeed increase yields in cotton without negatively impacting fiber quality. Past research studies have been substantiated by the rapid adoption of hybrid production systems in China and India. These hybrid production systems highlight the successful commercialization of heterosis to significantly increase yields. The current study demonstrates the existence of significant heterotic effects (nonadditive genetic effects) for agronomic traits in topcross progeny derived from modern and obsolete cultivars. Interestingly, the expression of these nonadditive genetic effects, calculated via midparent heterosis, was larger in topcrosses involving obsolete cultivars. Hence, this would indicate that obsolete cultivars have a greater ability to express nonadditive genetic effects in progeny than modern cultivars. The modern cultivar FiberMax 966 does not appear to follow this trend, as significant lint yield heterosis (39%) was identified in its topcross progeny with Georgia King. Clearly, FiberMax 966 represents a modern cultivar with tremendous potential for use in hybrid breeding efforts. With the exception of FiberMax 966, the modern cultivars included in this study have accumulated additive genetic effects through the breeding methods used in the last 100 yr. This is not too surprising, because early studies involving heterosis and hybrid cotton recommended that breeders concentrate efforts to accumulate additive genetic effects for genetic improvement because of the lack of a feasible hybrid seed production system (Lee et al., 1967; Meredith and Bridge, 1972). It has been documented that pure-line breeding has been the predominant method of developing new commercial cultivars during the last 50 yr (Bowman, 2000).

When considering the development of hybrid cotton, Miller and Lee (1964) concluded that the most efficient breeding method would take advantage of both additive and nonadditive gene action. Unfortunately, data from the current study and a previously conducted one (Meredith and Brown, 1998) show that increased genetic distance is not a good predictor of nonadditive gene effects. One breeding method proven to take advantage of both additive and nonadditive gene action is a reciprocal recurrent selection program. Probably the best example of the effectiveness of reciprocal recurrent selection has been documented in *Zea mays* L. through the use of the Iowa Corn Borer Synthetic no. 1 and Iowa Stiff Stalk Synthetic reciprocal recurrent selection populations (Hinze et al., 2005). In this type of system, the cotton breeder would need to choose

Table 5. Analysis of variance for fiber quality trait heterosis values (calculated as the heterotic effect divided by the midparent value multiplied by 100) of two groups of topcrosses consisting of five obsolete and five modern cotton cultivars grown in Alabama, North Carolina, and South Carolina in 2006.

Source of variation	df	Mean square					
		Length	Strength	Elongation	Uniformity index	Micronaire	Short fiber content
Location	2	2.46	16.42	83.57*	0.89	60.25*	14.33
Group	1	5.36	6.46	24.58	1.84	38.29	146.20
Entries(group)	8	4.98	47.90**	49.61	0.22	40.56*	25.01
Error	18	3.98	8.68	24.46	0.76	14.99	42.70
Mean heterosis obsoletes, %		1.3	0.2	−2.0	−0.1	−0.1	−1.1
Mean heterosis moderns, %		0.5	−0.7	−3.9	−0.5	2.0	3.3

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

the two populations that show useful heterosis for the initial phase of this program. The results of the current study suggest that breeders might consider using obsolete cultivars to maximize heterotic effects. Currently, this recommendation would be most applicable to cotton breeders in countries with adequate methods and resources to produce hybrid cotton seed. Most breeders may be hesitant to use obsolete cultivars in the production of pure lines due to inadequacies in many traits compared with modern cultivars, especially lint yield. This study revealed, however, that the F_1 hybrids of obsolete cultivars had desired levels of several traits approaching the levels of the modern F_1 hybrids evaluated. Historically, the obsolete cultivars have been most valuable in providing specific characters for achieving specific objectives (e.g., fiber strength, smooth leaf, and disease, insect, and nematode resistance). Perhaps obsolete cultivars possess additional sources of nonadditive genetic effects that can be exploited in a hybrid production system.

Acknowledgments

Special thanks to Cotton Incorporated for providing high-volume instrumentation fiber quality testing. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

References

Al-Rawi, K.M., and R.J. Kohel. 1969. Diallel analyses of yield and other agronomic characters in *Gossypium hirsutum* L. Crop Sci. 9:779–783.

Bowman, D.T. 2000. Attributes of public and private cotton breeding programs. J. Cotton Sci. 4:130–136.

Bowman, D.T., O.L. May, and D.S. Calhoun. 1997. Coefficients of parentage for 260 cotton cultivars released between 1970 and 1990. U.S. Gov. Print. Office, Washington, DC.

Bridge, R.R., and W.R. Meredith, Jr. 1983. Comparative performance of obsolete and current cotton cultivars. Crop Sci. 23:949–952.

Bridge, R.R., W.R. Meredith, Jr., and J.F. Chism. 1971. Comparative performance of obsolete varieties and current varieties of upland cotton. Crop Sci. 11:29–32.

Calhoun, D.S., D.T. Bowman, and O.L. May. 2006. Pedigrees of upland and pima cotton cultivars released between 1970 and 1990. Bull. 1155. Miss. Agric. and For. Exp. Stn., Mississippi State.

Culp, T.W. 1984. Comparative performance of obsolete and current Pee Dee germplasm lines of cotton. p. 98. *In* J.M. Brown (ed.) Proc. Beltwide Cotton Prod. Res. Conf., Atlanta, GA. Natl. Cotton Council of America, Memphis, TN.

Davis, D.D. 1978. Hybrid cotton: Specific problems and potentials. Adv. Agron. 30:129–147.

Dong, H., W. Tang, and D. Zhang. 2004. Development of hybrid *Bt* cotton in China: A successful integration of transgenic technology and conventional techniques. Curr. Sci. 86:778–782.

Dong, J., F. Wu, Z. Jin, and Y. Huang. 2006. Heterosis for yield and some physiological traits in hybrid cotton Cikangza. Euphytica 151:71–77.

Dongre, A., and V. Parkhi. 2005. Identification of cotton hybrid through the combination of PCR based RAPD, ISSR, and microsatellite markers. J. Plant Biochem. Biotechnol. 14:53–55.

Hinze, L.L., S. Kresovich, J.D. Nason, and K.R. Lamkey. 2005. Population genetic diversity in a maize reciprocal recurrent selection program. Crop Sci. 45:2435–2442.

Lee, J.A., P.A. Miller, and J.O. Rawlings. 1967. Interaction of combining ability effects with environments in diallel crosses of upland cotton (*Gossypium hirsutum* L.). Crop Sci. 7:477–481.

Marani, A. 1968. Heterosis and F2 performance of intraspecific crosses among varieties of *Gossypium hirsutum* L. and of G. *barbadense* L. Crop Sci. 8:111–113.

Meredith, W.R., Jr. 1984. Quantitative genetics. p. 132–147. *In* R.J. Kohel and C.F. Lewis (ed.) Cotton. Agron. Monogr. 24. ASA, CSSA, and SSSA, Madison, WI.

Meredith, W.R., Jr. 1990. Yield and fiber-quality potential for second-generation cotton hybrids. Crop Sci. 30:1045–1048.

Meredith, W.R., Jr., and R.R. Bridge. 1972. Heterosis and gene action in cotton, *Gossypium hirsutum* L. Crop Sci. 12:304–310.

Meredith, W.R., Jr., and R.R. Bridge. 1973. The relationship between F2 and selected F3 progenies in cotton (*Gossypium hirsutum* L.). Crop Sci. 13:354–356.

Meredith, W.R., Jr., and J.S. Brown. 1998. Heterosis and combining ability of cottons originating from different regions of the United States. J. Cotton Sci. 2:77–84.

Miller, P.A., and J.A. Lee. 1964. Heterosis and combining ability in varietal top crosses of upland cotton, *Gossypium hirsutum* L. Crop Sci. 4:646–649.

Olvey, J.M. 1986. Performance and potential of F2 hybrids. p. 101–102. *In* T.C. Nelson (ed.) Proc. Beltwide Cotton Prod. Res. Conf., Las Vegas, NV. Natl. Cotton Council of Am., Memphis, TN.

SAS Institute. 2002. The SAS system for Windows. Release 9.1. SAS Inst., Cary, NC.

Tang, B., J.N. Jenkins, J.C. McCarty, and C.E. Watson. 1993a. F2 hybrids of host plant germplasm and cotton cultivars: I. Heterosis and combining ability for lint yield and yield components. Crop Sci. 33:700–705.

Tang, B., J.N. Jenkins, J.C. McCarty, and C.E. Watson. 1993b. F2 hybrids of host plant germplasm and cotton cultivars: II. Heterosis and combining ability for fiber properties. Crop Sci. 33:706–710.

Wells, R., and W.R. Meredith, Jr. 1984a. Comparative growth of obsolete and modern cultivars: I. Vegetative dry matter partitioning. Crop Sci. 24:858–862.

Wells, R., and W.R. Meredith, Jr. 1984b. Comparative growth of obsolete and modern cultivars: II. Reproductive dry matter partitioning. Crop Sci. 24:863–868.

Wells, R., and W.R. Meredith, Jr. 1984c. Comparative growth of obsolete and modern cultivars: III. Relationship of yield to observed growth characteristics. Crop Sci. 24:868–872.

White, T.G., and R.J. Kohel. 1964. A diallel analysis of agronomic characters in selected lines of cotton, *Gossypium hirsutum* L. Crop Sci. 4:254–257.

White, T.G., and T.R. Richmond. 1963. Heterosis and combining ability in top and diallel crosses among primitive, foreign, and cultivated American upland cottons. Crop Sci. 3:58–62.

Wu, Y.T., J.M. Yin, W.Z. Guo, X.F. Zhu, and T.Z. Zhang. 2004. Heterosis performance of yield and fibre quality in F1 and F2 hybrids in upland cotton. Plant Breed. 123:285–289.

Young, E.F., and J.C. Murray. 1966. Heterosis and inbreeding depression in diploid and tetraploid cottons. Crop Sci. 6:436–438.