COTTON IMPROVEMENT

Cotton Germplasm Diversity and Its Importance to Cultivar Development

George Van Esbroeck and Daryl T. Bowman*

INTERPRETIVE SUMMARY

Germplasm diversity is of concern to breeders, as it should be to producers. Breeders rely on genetic variation between parents to create unique gene combinations necessary for new superior cultivars. Extensive use of closely-related cultivars by producers could result in vulnerability to pests and diseases. The importance of genetic diversity to crop vulnerability is widely recognized, however, there are conflicting views concerning the importance of genetically-distant parents to cultivar improvement. According to quantitative genetic theory, the probability of producing unique genotypes increases in proportion to the number of genes for which parents differ (genetic distance). However, past success in developing high-yielding cultivars from the matings of closely-related parents has led some to question the importance of genetically-diverse parents to crop improvement. Although the choice of parents is often the most important decision in a breeding program, little is known about the importance of parental genetic distance to successful cotton cultivar development. The objective of this study was to determine the importance of parental genetic distance to cotton cultivar development. Such information could be useful in identifying optimal breeding strategies for cotton improvement.

Successful cultivars, defined as cultivars planted to 1% or more of the total cotton acreage (more than 100 000 acres) for at least 1 yr from 1987 to 1996, were identified. Pedigrees were examined and the genetic relatedness between the parents of these cultivars was estimated as coefficient of parentage. The coefficient of parentage ranges from 0 for unrelated parents to 1 for two identical parents. For a self-pollinated species such as cotton, cultivars sharing one parent would have a coefficient of parentage of 0.5.

Sixty successful cultivars were identified. These occupied an average of 89% of the annual cotton acreage. The majority of the successful cultivars (60%) was derived from two-way crosses, primarily between cultivars, or between cultivars and experimental / germplasm lines. About 25% were reselections from existing cultivars and the remaining 15% were the result of complex crosses (crosses involving F_1 hybrids or sister lines).

The average coefficient of parentage between parents used in the final cross was 0.29 and was greater than what was expected by chance pairing (coefficient of parentage = 0.09). Further evidence that cultivar improvement could be made with crosses involving closely-related individuals was the large number of cultivars developed by reselection within cultivars. For example, a series of reselections starting from early 1900 cultivar, Lone Star, have resulted in cultivars with almost double the yield as the original cultivar, Lone Star. These yield gains were similar to gains for cultivars developed during this period through a series of crosses and intercrosses. Moreover, several recently-released, successful cultivars (Stoneville 474 and Suregrow 125) were developed by extensive intermating and backcrossing of closely-related lines. Although successful cultivars were developed from both distantly-related and closely-related cultivars, the large number of cultivars developed as reselections, or from the crossings of closely-related parents, indicated that there was sufficient variability or mechanisms to create variability in closely-related lines to make breeding progress.

The greater-than-expected-frequency of cultivars with closely-related parents suggests that distantly-related germplasm was unadapted and matings were, for the most part, restricted to genetically similar regionally-adapted lines. Other studies have shown that many generations of

Dep. of Crop Science, Box 8604, North Carolina State University, Raleigh NC 27695-8604. Received 24 Feb. 1998.
*Corresponding author (daryl_bowman@ncsu.edu).

reselection of unadapted germplasm may be needed to make such germplasm as productive as regionally-adapted cultivars. The problem of introgressing desirable traits from distantly-related germplasm was illustrated by the infrequent use of cotton germplasm resources. Of the 668 cotton germplasm lines registered in *Crop Science* during 1972 to 1996, only four (0.3%) appeared in the pedigrees of successful cultivars. However, the few diverse germplasm lines that were introgressed into agronomically suitable germplasm became widely used; almost all 60 successful cultivars contained some exotic germplasm in their pedigrees. Despite the wide-scale attempts to collect and develop a diverse germplasm base, the bulk of the cotton genetic resources has not been used. A greater concentration on quality rather than of quantity of diverse germplasm may offer greater rewards in crop improvement and reduced genetic vulnerability. Unless progress is made in transferring useful allelic variation from diverse to adapted germplasm without negative agronomic effects, germplasm resources will probably remain underused and the trend towards increased genetic vulnerability will continue.

ABSTRACT

Although it is widely assumed that genetically diverse parents facilitate the creation of superior progeny, few studies have examined the relationship between parental genetic distance and the creation of successful cultivars. In theory, matings of distantly-related parents will produce a greater number of transgressive segregates than matings of closely-related parents. However, for many crops, yield improvements have come from matings of closely-related genotypes. The objective of this study was to determine the relationship between parental genetic distance and development of successful cotton (*Gossypium hirsutum* L.) cultivars. Pedigrees of cultivars that occupied more than 1% of the total U.S. plantings for at least 1 yr from 1987 to 1996 were examined, and the genetic relatedness of the parents in the final cross was estimated as coefficient of parentage. A total of 60 successful cultivars was identified. The majority of these cultivars was derived from two-way crosses (60%), whereas the remainder were the result of reselections within cultivars or germplasm lines (25%), or complex crosses (15%). The average coefficient of parentage between parents used in the final cross was 0.29. This value was greater than was expected with random pairing of parents (coefficient of parentage = 0.09). In general, the genetic distance for parents of successful cultivars reflected the level of diversity within the regionally-adapted cultivars. Although many germplasm lines were available to breeders, use of diverse germplasm appeared to be restricted to a few agronomically-suitable lines. Of the 668 cotton germplasm lines registered in *Crop Science* during 1972 to 1996, only four (0.03%) appeared in the pedigrees of successful cultivars. The high frequency of successful cultivars derived from reselections, and the occurrence of several widely-grown cultivars that were developed from closely-related parents, indicated that genetically diverse parents have not been imperative to cotton cultivar improvement in recent years.

Interest in genetic diversity is twofold. First, genetic heterogeneity limits vulnerability to pests and diseases; second, it provides an ample supply of allelic variation that can be used to create new favorable gene combinations. Although the importance of genetic diversity to crop vulnerability is widely acknowledged (Duvick, 1984; Cox et al., 1986), there are conflicting reports as to the importance of genetically diverse parents to cultivar improvement. According to quantitative genetic theory, the genetic variance, and hence the probability of producing transgressive segregates, increases in proportion to the number of loci for which parents carry different alleles. This theoretical concept is supported by some studies that showed larger genetic variances among the progeny of distantly-related than of closely-related parents. For soybean [*Glycine max* (L.) Merr.], Manjarrez-Sandoval et al. (1997) observed that genetic variance for yield was positively associated with parental genetic distance, and that genetic variance declined to near zero when the coefficient of parentage was above 0.27. In studies with oat (*Avena sativa* L.), genetic variance was positively, albeit weakly, associated with genetic distance (Cowen and Frey, 1987). Helms et al. (1997), however, reported that genetic distance for several soybean lines was not associated with genetic variance and was not of sufficient predictive value for any combination of parents. Kisha et al. (1997) observed generally larger genetic variances for related soybean parents than for closely-related

parents, but concluded that genetic distance could not accurately predict the genetic variance for any given cross. In studies with wheat (*Triticum aestivum* L.), Souza and Sorrells (1991) and Cox and Murphy (1990) reported that the relationship between genetic distance and variance varied among traits and populations.

Inconsistent relationships between genetic distance and genetic variance, as well as success in developing high-yielding cultivars from the matings of closely-related parents, have led some to question the importance of genetically diverse germplasm to crop improvement. In barley (*Hordeum vulgare* L.), only a few germplasm sources have contributed to almost all yield advances (Rasmussen and Phillips, 1997). Extensive use of the hard red winter-wheat cultivar, Turkey, resulted in many years of crop improvement (Cox et al., 1986). In soybean, more than 80% of the gene pool was traced to as few as 10 plant introductions (Delannay et al., 1983).

Cultivar improvements achieved within closely-related populations have several possible explanations. For many crops, leading adapted cultivars have been intercrossed to such an extent that a cross involving distantly-related parents requires the use of unadapted germplasm. Unadapted genotypes usually contain a large number of undesirable genes or gene combinations, and it can take many generations of selection for unadapted germplasm to be as productive as adapted cultivars (Vello et al., 1984; Sneller et al., 1997); therefore, breeders frequently limit their efforts to a narrow range of adapted lines that may be more likely to produce gains in the short term. Some question the wisdom of this strategy and suggest that this concentration within a narrow germplasm base has led to a leveling off of yield gains (Sorrells and Wilson, 1997). Alternatively, it has been argued that, for traits controlled by multiple alleles, numerous mechanisms exist to create new genetic variation such that diverse parents are not necessary for the creation of transgressive segregates (Rasmussen and Phillips, 1997). Evidence for this viewpoint is the continued selection gain for quantitative traits in closed populations of maize (*Zea mays* L.) despite numerous cycles of recurrent selection (Dudley and Lambert, 1992).

The choice of parents is often the most important decision in a breeding program. The narrowness of the cotton genetic base (May et al., 1995; Van Esbroeck et al., 1998) and limited progress in cultivar improvement have led some to advocate that cotton breeders expand the range of germplasm used in crosses (Meredith, 1991). Considerable resources have gone into collecting, developing, evaluating, and maintaining germplasm resources, and there is now a large amount of diverse cotton germplasm available (Percival and Kohel, 1990). Moreover, the pedigrees of cotton cultivars and germplasm lines are well documented (Bowman et al., 1997; Calhoun et al., 1997; Van Esbroeck et al., 1997), allowing breeders to consider genetic distance of parents as a criterion in making crosses. However, the importance of parental genetic distance to successful cultivar development in cotton is not well understood. One way to determine the importance of genetically diverse parents to cultivar improvement is to examine the pedigrees of a large number of successful cultivars. The objectives of this study were to determine the importance of genetically diverse parents, as indicated by coefficient of parentage, to the development of successful cultivars. Such information may identify the breeding strategies that are most likely to produce improved progeny.

MATERIALS AND METHODS

We sought to examine parental coefficient of parentages for only those cultivars that exhibited superior agronomic performance. It was assumed that growers were aware of cultivar performance and, for the most part, grew superior cultivars. Data from the USDA- Agricultural Marketing Service (USDA, 1987-1996) were used to identify cultivars that were planted to 1% or more of the total cotton hectarage for at least 1 yr from 1987 to 1996. This was roughly equivalent to cultivars grown on more than 40 500 ha (100 000 acres). Pedigree information from Calhoun et al. (1997) was used to identify the parents of these cultivars. The genetic distance between the two parents used in the final cross was computed as coefficient of parentage (Kempthorne, 1969), using a modified FORTRAN program developed by D.M. Rodgers at Kansas

State University. In calculating coefficient of parentage, we used the assumptions of Bowman et al. (1997). These were that all ancestors were unrelated (coefficient of parentage = 0), cultivars obtained half their genes from each parent, all parents were homozygous and homogeneous, and the coefficient of parentage between the two parents of a reselection was 0.5 [a compromise between a self-pollination (coefficient of parentage = 1) and a cross to an unknown (coefficient of parentage = 0.0)]. For reselections, the coefficient of parentage between the parents involved in the original crosses was also calculated. This was done to exclude the possibility that the original cultivars were not homozygous (many cultivars are released at an F_6 or earlier generation) and the success of their selection involved further gene segregation. Cultivars or germplasm lines with unknown pedigrees were excluded from the analysis.

The area of adaptation (or selection) for the parents of successful cultivars was also examined. For this purpose we considered three general areas of adaptation: Eastern (Mississippi delta and southeastern USA), Central (Texas), and Western (Arizona, California, and New Mexico). Because genetic distance among parents used in a breeding program can be influenced by the coefficient of parentage between the available regionally-adapted cultivars or germplasm lines, we also examined the hypothetical (expected) coefficient of parentage between parents assuming that all parents were randomly crossed. To do this, we calculated the coefficient of parentage between each parent and all others and then determined the frequency of each coefficient of parentage class as a percentage of the total number of hypothetical crosses.

RESULTS AND DISCUSSION

Sixty cultivars, that were grown on more than 1% (40 500 ha) of the total cotton hectarage in at least 1 yr from 1987 to 1996, were identified as successful cultivars. These cultivars, originating from breeding efforts in the 1970s and 1980s, accounted for an average of 89% of the total annual U.S. land area planted to upland cotton. Sixty percent of these cultivars was derived from two-way crosses between cultivars or between cultivars and germplasm lines. About 25% of the successful
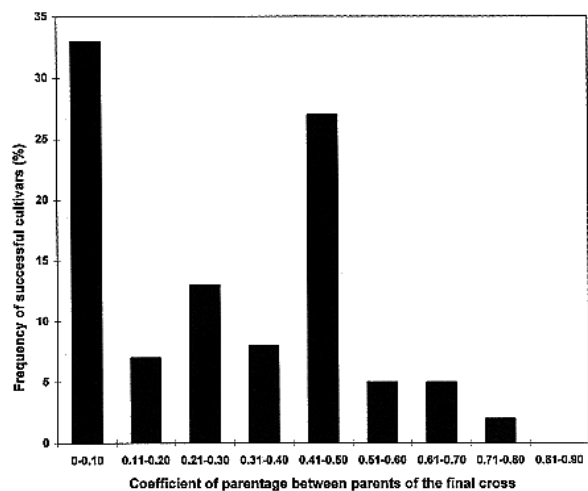

Figure 1. Frequency (%) of successful cultivars vs. coefficient of parentage between parents used in the final cross.

cultivars were reselections from existing cultivars, a value similar to the frequency of reselections (31%) reported for the 285 upland cultivars released from 1970 to 1990 (Bowman et al., 1996). The remaining 15% were derived from complex crosses (crosses involving F_1 hybrids or sister lines).

The coefficient of parentage between parents used in the final cross for successful cultivars ranged from 0 to 0.875, with a mean of 0.29 (Fig. 1). The high frequency of values around 0.5 was due to the large number of cultivars derived from reselections and the assumption that the coefficient of parentage between the two parents of a reselection was 0.5. However, when reselections within a cultivar were considered to be derived as progeny of the original cross, the average coefficient of parentage between parents used in the final cross was 0.18.

The average coefficient of parentage for all possible pairwise combinations of parents of the successful cultivars was 0.09, a value similar to the average relationship (0.07) among all cultivars released between 1970 and 1990 (Bowman et al., 1996). Thus, regardless of how coefficient of parentage was calculated for parents of reselections, the genetic relatedness of the combination of parents used to create successful cultivars (coefficient of parentage = 0.18 or 0.29) was greater than the average relatedness among all possible pairs of parents (coefficient of parentage = 0.09) (Fig. 2).
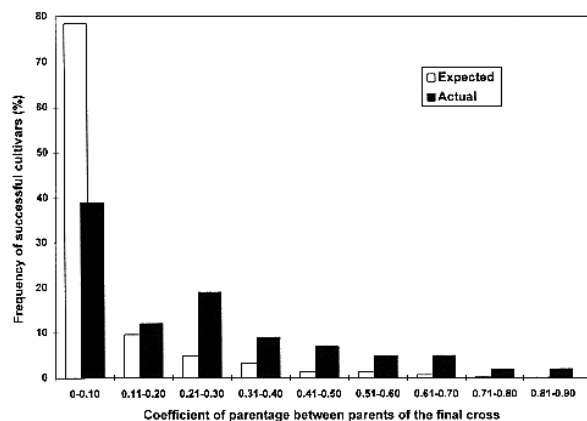
Figure 2. Relationship between the coefficient of parentage of parents used in the final cross and frequency of successful cultivars (Actual). Expected values represent the expected frequencies for each coefficient of parentage class if all parents were randomly crossed. Reselections were considered as a product of the original cross.

Parents of successful cultivars almost always originated in the same region. Excluding reselections, only four of the remaining 45 cultivars had an immediate parent outside its region. May et al. (1995) showed that although the average coefficient of parentage among 126 cotton cultivars released between 1980 and 1990 was low (0.07), the coefficient of parentage among regionally-adapted cultivars was as high as 0.34. Thus, the high frequency of closely-related parents in the final cross for successful cultivars reflects the fact that new cultivars were for the most part developed from high-yielding, closely-related, locally-adapted cultivars. Distantly-related germplasm is often unadapted, thus restricting parents to regionally-adapted lines; however, about one-third of the successful cultivars had parents that were distantly-related although locally adapted (Fig. 1).

In contrast to the widely held view that a large genetic distance among parents facilitates the development of superior progeny, we did not find such a consistent relationship. Successful cultivars were developed from both closely-related and distantly-related parents. However, successful cultivars had a greater than expected frequency of closely-related parents. It was assumed that this greater -than-expected frequency of closely-related parents reflected the genetic diversity within regionally-adapted cultivars.

The weak relationship between parental genetic diversity and cultivar improvement has several probable explanations. There may be sufficient allelic variation, mutation, or recombination in the mating of closely-related individuals to result in improved agronomic performance and /or coefficient of parentage may not reflect true genetic distance. The large number of successful cultivars developed as reselections indicates that there was sufficient recombination in matings of closely-related parents to improve agronomic performance. May et al. (1995) noted that although regionally adapted lines were closely related, they contained a wide range of diversity for maturity and fiber properties. Presumably the variation in several agronomically important traits among the regionally adapted lines offered a greater opportunity to quickly enhance a cultivar than the much greater total variation in unadapted germplasm. Further evidence that yield improvements have not been limited by matings of closely-related individuals is the number of cultivars developed as reselections and the improvements obtained through reselection. Yield trials with current and obsolete cultivars, together with pedigree data, show that a series of reselections starting from the early 1900 cv. Lone Star have resulted in cultivars that yield about twice as much as the original cultivar (Table 1). These yield gains were similar to gains for cultivars developed during this period through a series of crosses and intercrosses. Moreover, several recently-released, very successful cultivars were developed by extensive intermating and backcrossing of closely-related DES and Stoneville cultivars (Fig. 3). These results suggest that a minimal amount of recombination resulted in sufficient genetic variance to make breeding progress.

Table 1. Lint yield of cultivars developed through reselections starting from the cv. Lone Star.

Cultivar	Year of release	Yield		
		Wells and Meredith (1984)†	Bridge and Meredith (1983)‡	Bridge et al. (1971)
		--------------- kg ha-1 lint---------------		
Lone Star	1905	558		
Stoneville 2B	1938	674	713	861
Stoneville 213	1962	1118	1070	1201

† Yields are the means of 26 April and 12 May planting dates.
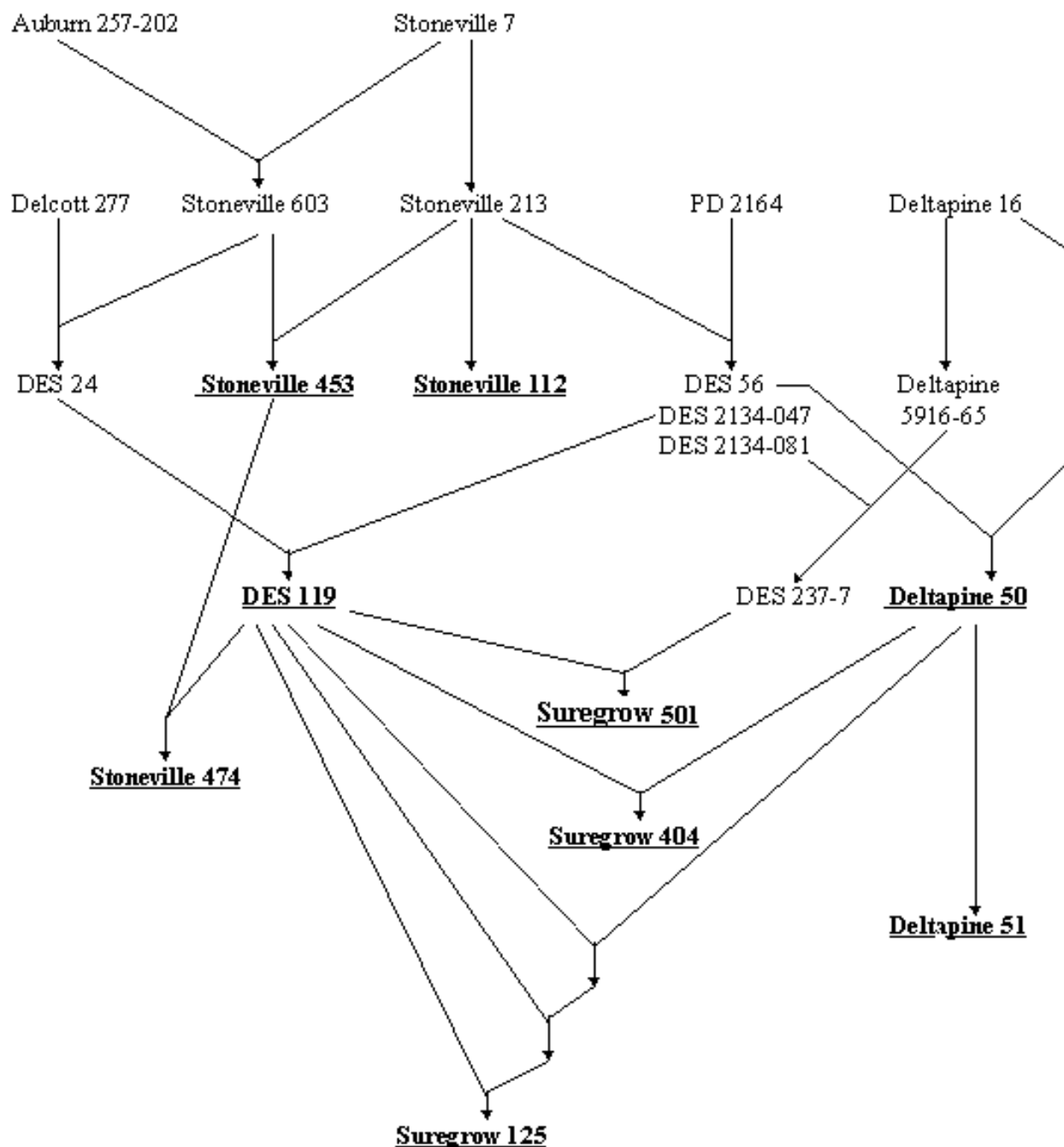
‡ Yields are the mean of 2 yr.

Figure 3. Pedigrees for several successful cultivars showing a large number of reselections and crossings to related cultivars. Cultivars in bold occupied more than 1% of the U.S. cotton-growing area in at least 1 yr from 1987 to 1996.

Studies on F_2 heterosis provide additional support for the view that improvements can be made from the mating of closely-related individuals. F_2 heterosis has been used to identify parents that produce high numbers of superior inbred lines. For wheat, Cregan and Busch (1977) reported that the yields from the F_2 bulk generation were highly correlated ($r = 0.81$) to F_5 line means and concluded that bulk F_2 yields were effective in predicting material from which the highest-yielding inbred lines were derived. For cotton, Green and Culp (1989) reported a positive correlation ($r = 0.58$) between F_2 yields and the number of superior lines selected per cross. There are few studies that

have directly examined the relationship between F_2 heterosis and genetic distance in cotton. However, several studies have shown that very high levels of F_2 heterosis may be attained from the matings of closely-related lines. For example, in a study involving 64 F_2 hybrids obtained from 20 parents, highest lint yields and second highest heterosis (17.9%) were obtained from the cross of the closely-related (coefficient of parentage = 0.715) lines, Coker 315 and Delcot 344 (Tang et al., 1993). This further substantiates the conclusion that recombination in key areas of the genome may be of greater importance to crop improvement than genetic distance per se.

A second possible explanation for the weak relationship between diverse parental coefficient of parentage and cultivar success is that coefficient of parentage may not reflect true genetic distance. In calculating coefficient of parentage, it was assumed that a cultivar inherits 50% of its alleles from each parent. Recent molecular marker data, however, indicate that under intense selection this value may deviate by 20% (Bernardo et al., 1996). Attempts to improve estimates of genetic distance with morphological features or molecular markers have led to limited success. These distance estimates are also problematic; limited polymorphism may be a disadvantage for morphological divergence, while time and resources often limit collection of molecular marker data. For soybean, Kisha et al. (1997) observed that the molecular marker estimates of genetic distance were sometimes a better predictor of genetic variance than coefficient of parentage. However, results varied among populations and traits. In wheat, Cox and Murphy (1990) reported that combined estimates of genetic distance improved the relationship between genetic distance and variance, however, coefficient of parentage was the single best predictor of genetic variance or heterosis.

Greater genetic variance among the progeny of distantly-related than closely-related parents is expected due to greater recombination; however, recombination rates are not necessarily proportional to genetic distance. In several plant species, specific genes exist that influence recombination rate (Baker et al., 1976). In soybean, Lorenzen et al. (1996) observed that the number of recombinations varied with cultivar. In some cases, large portions

of the genome were inherited intact from a single parent. It may be that recombination in key areas of the genome is of greater importance than total recombination per se. Furthermore, recombination rates in distantly-related genotypes may be reduced because of improper pairing during meiosis due to extensive differences in DNA sequences. Ganal and Tanksley (1996) reported reduced recombination in interspecific in comparison to intraspecific crosses of *Lycopersicon.* Souza and Sorrells (1991) reported an initial increase in genetic variance or hybrid vigor with increasing genetic distance followed by decline at high genetic distance. This suggests that recombination may be restricted at high genetic distance or that the progeny of wide crosses were unable to fully express their yield potential.

For cotton, the major constraint to the use of genetically-diverse parents is that they tend to be from different regions and as such unadapted. High recombination between adapted and unadapted parents can break up favorable linkage groups such that progenies no longer contain the favorable allele combinations. Moreover, tropical accessions often contain unfavorable linkage groups such that it may take up to 14 generations of backcrossing to obtain lines with suitable fiber properties (Percival and Kohel, 1990). Evaluations of commercial by exotic cotton crosses often show reduced yields relative to commercial cultivars (McCarty et al., 1996; Tang et al., 1993). For example, although root-knot nematode [*Meloidogyne incognita* (Kofoid and White) Chitwood] causes major yield losses in cotton, incorporation of resistance from exotic germplasm has been limited because crosses between elite lines and resistant lines exhibited large yield reductions (Robinson et al., 1997). Furthermore, introgression of exotic germplasm for cotton may be delayed because of the need to simultaneously select for a range of fiber properties. The practical use of diverse cotton germplasm appears to be similar to that of many other crops where very diverse germplasm requires numerous cycles of selection to be of value (Vello et al., 1984).

The problem of introgressing desirable traits from distantly-related germplasm is illustrated by the infrequent use of cotton germplasm resources. Only four (0.3%) of the 668 cotton germplasm lines

registered in *Crop Science* during 1972 to 1996 (Van Esbroeck et al., 1997) appeared in the pedigrees of successful cultivars in this study. This statistic undoubtedly underestimates the importance of germplasm resources, as recently developed (e.g., 1990+) germplasm may not yet have been introgressed into cultivars. Furthermore, germplasm developed for regions with limited cotton hectarage was also not included. This statistic, however, highlights the limited use of the vast majority of cotton germplasm.

Limited use of germplasm, however, does not appear to indicate limited importance. When a few of these diverse germplasm lines were introgressed into agronomically suitable cultivars, they became widely used; almost all 60 successful cultivars contained some exotic germplasm in their pedigrees. This germplasm was primarily incorporated through crosses with lines containing triple hybrid germplasm (AXTE, Delcot 277, and PD 2165) or Bar 4/16 SAKEL (Tamcot SP21, SP23, and SP37). Despite the wide-scale attempts to collect and develop a diverse germplasm base, the bulk of the cotton genetic resources has not been used. A greater effort to introgress diverse germplasm into regionally adapted cultivars that do not carry a yield penalty may offer greater rewards in crop improvement and reduced genetic vulnerability.

Rasmussen and Phillips (1997) suggested that the gap in the gene frequencies between improved and unimproved gene pools was now so large that it essentially precludes obtaining improved cultivars from wide crosses. Because of these large differences in agronomic suitability between very diverse germplasm, use of exotic germplasm for many crops is now limited to traits such as disease resistance that are controlled by very few genes (Sorrells and Wilson, 1997). To avoid negative effects of crossing to distantly-related unadapted germplasm, Cox and Murphy (1990) advocated first looking at mean yield and identifying superior cultivars with subsequent consideration of genetic distance. Sorrells and Wilson (1997) advocated parent building, the gradual incorporation of a few traits through some form of backcrossing or marker-assisted selection to make use of allelic variation in distantly-related germplasm. A few sources of exotic germplasm have been introgressed into adapted cultivars. Their frequent use is evidence that diverse germplasm may be used to improve cotton varieties.

In conclusion, we observed that parental genetic diversity, as estimated by coefficient of parentage, was not imperative for cotton improvement. Successful cultivars were most frequently developed from closely-related parents, with a level of diversity similar to the average genetic relationship among regionally-adapted cultivars. The large number of cultivars developed from closely-related parents indicated that there was sufficient variability or mechanisms to create variability, to make breeding progress in a narrow germplasm base. Unless methods are improved to transfer useful allelic variation from diverse to adapted germplasm without negative agronomic effects, cotton germplasm resources will remain largely underused and the trend towards increased genetic uniformity will probably continue.

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