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Changes in the Genetic Diversity of Cotton in the USA from 1970 to 1995

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ABSTRACT

Despite concern about genetic vulnerability, little is known about the recent changes in the genetic diversity of upland cotton (*Gossypium hirsutum* L.). The objectives of this study were to determine the trends in the genetic diversity of upland cotton in the USA during the last 25 yr and to investigate probable causes for these changes. Two estimates of genetic diversity, coefficient of parentage (r_p) and field uniformity (r_f ; r_p weighted by the proportion of the hectare occupied), were made for cultivars occupying over 1% of the hectare within a region (Southeast, South-central, Southwest, and West) from 1970 to 1995 at 5-yr intervals. An average of 17 (range = 8–46) cultivars accounted for 97% of the cotton hectare within a region. Regional r_p values were relatively stable at 0.12 to 0.15 from 1970 to 1990 and then sharply increased to 0.20 in 1995. Higher r_p values in commonly grown cultivars than in released cultivars indicated that much of the genetic diversity in cotton remains unused by growers. Field uniformity (r_f) remained at about 0.30 for all regions during the past 25 yr because increases in r_p were matched with an increase in the number of cultivars grown and/or a decline in the proportion of the area planted to any single cultivar. The frequent use of several parents for the creation of new cultivars and the planting of only a small portion of the available cultivars has led to a high level of genetic uniformity.

LACK OF GENETIC DIVERSITY in crop species has long been recognized as a potential threat to sustaining high yields (National Academy of Sciences, 1972; Hammons, 1976; Walsh, 1981). Genetic uniformity can hasten the buildup of virulent biotypes and lead to large crop losses if there is uniform susceptibility to a pest or disease. The use of genetically diverse parents in a breeding program may alleviate this problem and also increase the number of transgressive segregates for yield (Rodgers et al., 1983; Cowen and Frey, 1987). Thus, genetic diversity ensures a measure of protection against future disease or insect epidemics and provides a basis for future genetic gains.

Genetic uniformity within a crop may be caused by the extensive use of one or more closely related cultivars. The relatedness of cultivars is frequently expressed as the coefficient of parentage (r) which is defined as the probability that the alleles at a random locus in two cultivars are identical by descent (Kempthorne, 1969). The coefficient of parentage has been widely used to measure genetic diversity in crop species (Rodgers et al., 1983; Cox et al., 1986; Souza and Sorrells, 1989; Knauft and Gorbet, 1989; Gizlice et al., 1993; May et al., 1995). Cox et al. (1986) weighted the pairwise r values of commercially important cultivars by the proportion of the hectare occupied by each. They defined this weighted value as field uniformity. Field uniformity estimated the coefficient of parentage of any two plants selected at random within the region where the cultivars

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were grown commercially. In winter wheat (*Triticum aestivum* L.), field uniformity was frequently larger than mean r among all cultivars because much of the hectareage consisted of a few closely related cultivars.

Bowman et al. (1996) reported that 260 upland cotton cultivars released between 1970 and 1990 had a higher level of diversity ($r = 0.07$) than wheat, barley (*Hordeum vulgare* L.), oat (*Avena sativa* L.), peanut (*Arachis hypogea* L.), and soybean [*Glycine max* (L.) Merr.], where r ranged from 0.13 to 0.42 (Rodgers et al., 1983; Murphy et al., 1986; Martin et al., 1991; Knauff and Gorbet, 1989; Gizlice et al., 1993). Although the number of cotton cultivars released is large, the number available to growers is often limited by regional adaptability, seed availability, seed quality or seed cost. Crop estimates show in some regions over half of the cotton hectareage is planted to a single cultivar, indicating a potentially high level of field uniformity (USDA, 1995).

Despite widespread concern about genetic vulnerability and the importance of monitoring trends in crop genetic diversity, little information is available on the changes in genetic diversity that may have occurred in cotton over the last 25 yr. The objectives of this study were to determine the coefficient of parentage and field uniformity for cotton from 1970 to 1995 in the USA and to investigate probable causes for any changes that might have occurred.

MATERIALS AND METHODS

Data for cultivars grown and the proportion of the hectareage occupied within each state and totals for the USA were obtained for the years 1970 to 1995 at 5-yr intervals (USDA 1970, 1975, 1980, 1985, 1990, 1995). By means of cotton planting statistics supplied by the National Agricultural Statistics Service, data were summarized for four regions—Southeast (Alabama, Florida, Georgia, North Carolina, and South Carolina), South-central (Arkansas, Louisiana, Mississippi, Missouri, and Tennessee), Southwest (Oklahoma and Texas), and West (Arizona, California, and New Mexico). Coefficient of parentage (r_p) and field uniformity (r_f) was calculated for cultivars occupying more than 1% of the hectareage of each region and across the USA. Pedigree information, r calculations, and assumptions were as described by Bowman et al. (1997). Average coefficients of parentage (r_p) for a region were obtained by averaging all pairwise r values. Field uniformity was calculated as the summation of all possible pairwise r values multiplied by the proportion of the plantings occupied by each cultivar (Cox et al., 1986). The r_f values included the probability of sampling a cultivar twice. Since the r_p of a cultivar sampled twice is assumed to be 1, r_f values are highly influenced by cultivars occupying a large proportion of the plantings. For example, a cultivar occupying 50% of the hectareage would contribute 0.25 to r_f . Cultivars for which the pedigree information was unavailable were considered as unknowns. To account for plantings to unknown cultivars, we divided the fraction of hectareage occupied by unknown cultivars by the number of unknowns listed (USDA, 1970, 1975, 1980, 1985, 1990, 1995) and assumed an average r_p value of 0.07 among unknowns and between unknowns and known cultivars (Bowman et al., 1996).

For 1970 and 1995 the pedigrees of the cultivars were examined, and the genetic contribution of frequently used germplasm to the cultivars was determined. Genetic contributions to the final cross of widely grown cultivars were assessed for

various sources of breeding material. This was carried out for each 5-yr interval in the study.

RESULTS AND DISCUSSION

An average of 17 (range = 8–46) cultivars occupied 97% of the cotton hectareage within a region from 1970 to 1995 (Table 1). Mean regional coefficient of parentage (r_p) ranged from 0.12 to 0.15 during 1970 to 1990 and then sharply increased to 0.20 in 1995 (Table 2). These values were higher than the average r of 0.07 reported for 260 cotton cultivars released between 1970 and 1990 (Bowman et al., 1996), indicating that much of the diversity available in the germplasm is not widely utilized.

The Southeast and South-central regions, which occupy about 20 and 30% of the total U.S. cotton hectareage, respectively, were the most genetically uniform regions ($r_p = 0.26$ – 0.28 in 1995). The Southwest and West regions which contain about 40 and 10%, of the total hectareage, respectively, were the most diverse, each with 1995 r_p values of 0.15. The r_p values for the USA as a whole were lower than regional values, because eastern and western cultivars tend to be genetically diverse from each other (May et al., 1995).

Changes in breeding strategies over the past 25 yr appear to account for the decline in the genetic diversity of cotton. In 1970, in-house germplasm was extensively utilized for the development of new cultivars (Fig. 1). Reselections were common with 19 of the 29 cultivars in the USA in 1970 derived from reselecting within existing lines. The practice of utilizing closely related in-house germplasm decreased the diversity within breeding programs, but it helped maintain a high level of genetic diversity between cultivars from different programs. The genetic uniformity of the cultivars in 1970 ($r_p = 0.08$) resulted from several sources (Table 3). 'Lankart' and 'Paymaster 101' or selections from these cultivars were used as the parents for four cultivars. 'Lone Star 65', 'Macha', 'Empire', and 'Coker 100 Wilt' were frequent ancestors but contributed only 6 to 11% of the genetic material to the 29 widely grown cultivars.

After 1970 breeders began utilizing a common pool of elite public and private germplasm (Fig. 1), such that by 1995 r_p had risen to 0.16 with all frequently grown cultivars related to each other (r was >0 for all pairwise combinations). A few elite public and private cultivars from previous years were extensively utilized (Table 3). 'Deltapine 50', 'Deltapine Acala 90', 'DES 56', and

Table 1. The number of cultivars† per region and across the USA at 5-yr intervals from 1970 to 1995. Numbers in brackets indicate the percentage of the total hectareage accounted for.

Year	Region				USA
	Southeast	South-central	Southwest	West	
1970	16 (97)	9 (99)	25 (99)	9 (97)	30 (96)
1975	12 (98)	8 (97)	33 (99)	11 (97)	34 (93)
1980	15 (96)	11 (97)	32 (99)	10 (96)	36 (88)
1985	14 (98)	14 (99)	46 (99)	10 (96)	50 (98)
1990	14 (96)	10 (97)	29 (97)	16 (94)	30 (98)
1995	17 (92)	18 (96)	18 (99)	19 (96)	24 (89)

† Cultivars occupying at least 1% of the hectareage.

Table 2. Coefficient of parentage (r_p) among cultivars† in a region and across the USA at 5-yr intervals from 1970 to 1995.

Year	Region					Mean	USA
	Southeast	South-central	Southwest	West			
1970	0.23	0.14	0.07	0.03	0.12	0.08	
1975	0.15	0.14	0.09	0.10	0.15	0.08	
1980	0.16	0.19	0.09	0.13	0.14	0.09	
1985	0.18	0.25	0.08	0.11	0.16	0.08	
1990	0.17	0.22	0.12	0.12	0.15	0.08	
1995	0.28	0.26	0.15	0.15	0.20	0.16	

† Cultivars occupying at least 1% of the hectareage.

'DES 119' were each used as a parent for three widely grown cultivars. Moreover, a large proportion of the genes for many of the cultivars were derived from 'Deltapine 16', 'Stoneville 7', and DES 56. Deltapine 16 contributed an average of 28% of the genome of 13 cultivars. Stoneville 7, in the parentage of 'Stoneville 603', 'Stoneville 213', and DES 56, also had a large impact on r_p ; 13 cultivars obtained an average of 25% of their genes from this source. Nine cultivars obtained an average of 33% of their genes from DES 56.

The decline in diversity due to frequent use of a few parents was even more alarming when the actual numbers of hectares planted to each cultivar is considered. In 1995, 89% of the hectareage in the Southeast region and 50% of the hectareage in the USA was planted in cultivars with Deltapine 16 in their pedigree.

The hybridization of leading cultivars, followed by selection appears to have been a very successful breeding strategy. It is not clear from this study if commercial breeders concentrated on crosses involving a few agronomically superior cultivars or whether extensive crosses were employed and only those involving leading cultivars were agronomically successful. However, the extensive use of many of the same cultivars by numerous commercial breeders has resulted in the homogenization of cultivars and appears to have been the major factor contributing to the declining genetic diversity of cotton.

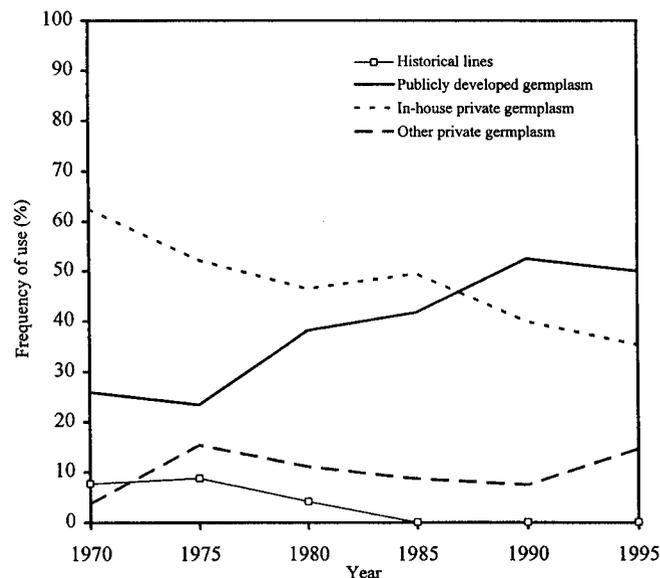


Fig. 1. Origin of parents used in the final cross for the development of cotton cultivars from 1970 to 1995.

The repeated use of many of the same parents may be attributed to proven yielding ability combined with a desirable phenotype. Use of Deltapine 16 appears to be primarily because of its widespread adaptability and secondarily as a source for the introgression of the smoothleaf trait (reduced or absent pubescence on the abaxial leaf surfaces), originating from 'Deltapine Smoothleaf'. The smoothleaf trait increases the lint grade by reducing the trash on lint (Lee, 1985). Extensive use of DES 56 stems from its yielding ability coupled with its earliness. Early maturity helps avoid late season crop losses due to infestations of the boll weevil (*Anthonomous grandis* Boheman) (Walker et al., 1977) and reduces input requirements for water, nutrients, and crop protectants (Niles and Feaster, 1984). Widespread occurrence of Stoneville 7 in the germplasm appears related to the proven yielding ability of Stoneville 213 and 603, both selections from Stoneville 7. 'Pee Dee 2164' was widely used as a source of high fiber strength (Meredith, 1991). During the 1980s, the fiber industry demanded higher strength cottons and there were few other adapted, high-strength lines available. The frequent use of the full sibs 'Tancot SP 21', '23' and '37' resulted from their resistance to multiple pests and diseases as well as their high yielding ability and earliness in certain environments. (Meredith, 1991).

Table 3. Frequency in the pedigree and genetic contribution of original germplasm to cultivars† grown in 1970 and 1995.

Germplasm‡	Number of occurrences in pedigrees	Mean genetic contribution§	Average r with all cultivars
		$r \times 100$	$r \times 100$
	#	1970 (29 cultivars)¶	
Lone Star 65	18	17.0	10.5
Paymaster 101	4	62.5	8.6
Macha	10	21.4	7.4
Lankart	4	53.9	7.4
Empire	6	30.5	6.3
Coker 100 Wilt	6	28.7	5.9
Texas Stormproof	4	40.4	5.5
Stoneville 7	2	75.0	5.2
Auburn 56	2	75.0	5.2
		1995 (24 cultivars)	
Deltapine 16	13	27.9	15.1
Stoneville 7	13	24.9	13.5
DES 56	9	33.3	12.5
Deltapine Smoothleaf	13	19.2	10.4
Pee Dee 2164	12	20.3	10.2
Deltapine 45	13	18.2	9.9
Tancot SP21,23,37	5	42.2	8.8

† Cultivars occupying at least 1% of the hectareage.

‡ Germplasm may be related to other germplasm listed in this table.

§ Average r value with cultivars in which germplasm occurs.

¶ One cultivar with an unknown pedigree was not included.

Table 4. Field uniformity (r_f) for cotton growing regions and across the USA at 5-yr intervals from 1970 to 1995.

Year	Region					Mean	USA
	Southeast	South-central	Southwest	West			
1970	0.33	0.43	0.17	0.35	0.32	0.17	
1975	0.27	0.44	0.16	0.42	0.32	0.13	
1980	0.27	0.39	0.13	0.35	0.29	0.10	
1985	0.25	0.35	0.13	0.35	0.27	0.12	
1990	0.31	0.42	0.14	0.25	0.28	0.14	
1995	0.35	0.38	0.20	0.36	0.32	0.18	

Although there are frequently several sources for desired traits, commercial breeders have extensively utilized germplasm where the trait has been incorporated into a high yielding adapted cultivar. For example, there are several sources for the smoothleaf trait, however, breeders have almost exclusively utilized Deltapine 16 for the introgression of this trait. Traits such as the smoothleaf, which are controlled by a single locus (Lee, 1985), could be introgressed through a backcross program. This approach would require a great deal more time and effort than crossing to an adapted line carrying the trait. For traits such as earliness, which are quantitatively inherited (Niles and Feaster, 1985), backcrossing would be more complex. This illustrates a need for finding other adapted sources of favorable alleles and for the incorporation of favorable alleles into a wide range of germplasm.

Field uniformity can be much greater than genetic uniformity if a few cultivars occupy a large proportion of the hectare. Regional field uniformity (r_f) has remained at about 0.30 for the past 25 yr despite an increase in r_p (Table 4). Values for the USA have fluctuated between 0.10 and 0.18. Field uniformity did not increase along with r_p because increases in r_p were matched by an increase in the number of cultivars (Table 1) and/or a decline in the proportion of the plantings occupied by the leading cultivars (Table 5). The Southeast and South-central region had the highest genetic uniformity (r_p). Also much of the hectare in these two regions was planted in a single cultivar resulting in highest r_f values. The Southwest region had both the lowest r_p and a large number of cultivars, resulting in a low r_f . Despite the high cultivar diversity in the Western region, about half of the plantings were to a single cultivar and field uniformity was high.

Leading cultivars occupied an average of 33% of the total cotton hectare within a region. A few cultivars have occupied large proportions of the hectare for many years and had the greatest impact on r_f . In the Southeast, 'Coker 201' or 'Coker 310' occupied up to 48% of the hectare in the 1970s and 1980s, whereas Deltapine Acala 90 accounted up to 39% of the hectare

Table 5. Proportion of the hectare (%) occupied by the most widely grown cultivar in a region and across the USA from 1970 to 1995.

Year	Region					USA
	Southeast	South-central	Southwest	West		
1970	41	48	24	48	26	
1975	25	46	12	59	17	
1980	20	27	11	51	8	
1985	24	30	12	47	11	
1990	39	41	15	29	17	
1995	18	20	33	53	14	

age in the 1990s. Deltapine 16 and Stoneville 213 each occupied about 40% of the cotton growing area in the South-central region in the 1970s and were later replaced by cultivars ('Deltapine 20' and Deltapine 50) related to Deltapine 16 and Stoneville 213. The Southwest region grew the greatest number of cultivars; 'Lankart 57' was most popular in the 1970s whereas in 1995 'Paymaster HS 26' and 'Paymaster HS 200' were the most frequently grown. In the West, primarily the San Joaquin Valley of California, the "one cultivar/one quality" concept restricted the number of cultivars available and 'Acala SJ1' or 'Acala SJ2' accounted for about half of the plantings for over 20 yr from 1970 to 1990. In 1995 'Acala Maxxa' occupied over half of the hectare.

In 1970, Deltapine 16 occupied 26% of the U.S. hectare, but since then the leading cultivar has occupied from 8 to 17% of the total hectare (Table 5). Overall r_f values for the USA fluctuated between 0.10 and 0.18 and were lower than the regional values, reflecting the regional differences in cultivars grown and the distinctiveness of the regional gene pools (May et al., 1995). In 1970, Deltapine 16 had the greatest influence on r_f , primarily a result of the high proportion of the hectare planted to this cultivar (Table 6). In 1995, Deltapine 50 and Paymaster HS 26 had the greatest influence on r_f . The large influence of Deltapine 50 was due to a combination of frequent plantings (10% of the hectare) and a high degree of relatedness ($r = 0.25$) to other cultivars. The large influence of Paymaster HS 26 resulted from it occupying a large portion of the hectare as it had a below average r with other cultivars.

Table 6. Leading contributors to field uniformity (r_f) in the USA in 1970 and 1995.

Cultivar	Proportion of the hectare occupied	Mean r with other cultivars	Contribution to r_f
		r_f	
%			
1970 (29 cultivars)‡			
Deltapine 16	26	0.08	46
Stoneville 213	16	0.08	21
Acala SJ-1	11	0.05	9
Lankart 57	8	0.09	6
Stoneville 7A	5	0.08	5
1995 (24 cultivars)			
Deltapine 50	10	0.25	18
Paymaster HS 26	14	0.06	14
Deltapine 51	7	0.20	11
Deltapine 20	6	0.20	9
Deltapine 5415	5	0.24	9
Deltapine 90	5	0.19	6

† Cultivars occupying at least 1% of the hectare.

‡ One cultivar with an unknown pedigree was not included.

These data, in conjunction with other studies (Bowman et al., 1996), show that cultivar diversity is no guarantee of field diversity. Despite considerably higher levels of genetic diversity in cotton than wheat, cotton production has been concentrated in a few cultivars and thus field uniformity in many years has been about the same for both crops (Cox et al., 1986). A factor contributing to widespread use of a few cultivars is the availability of superior cultivars with widespread adaptability. Because farmers very quickly learn which cultivars are most profitable, they rapidly switch plantings to a superior cultivar. For example, Deltapine 50 occupied 7% of the U.S. hecterage within 2 yr of its release.

The risks associated with today's high levels of genetic uniformity in cotton are not clear. The large number of released cultivars and germplasm, which could be put to use in a minimum amount of time, provide a considerable measure of protection from insect or disease epidemics (Duvick, 1984). In the past, some cotton cultivars were grown extensively for many years without becoming vulnerable to insects or disease. For example, Lankart 57 was widely grown in the Southwest for over 20 yr. Both Deltapine 16 and Stoneville 213 were grown in the South-central region for over 20 yr and appear frequently in the pedigrees of today's cultivars. Moreover, with few exceptions, cultivars did not become obsolete due to disease or insect susceptibility but were replaced as higher yielding germplasm became available. Exceptions to this lack of susceptibility have been the boll weevil invasion at the turn of the century and the recent whitefly (*Bemisia* spp.) epidemic in parts of the Western region. The absence of widespread disease or insect losses in many cotton growing regions despite high levels of genetic uniformity may be due to a combination of effective chemical control agents and sufficient levels of genetic resistance. However, reliance on chemicals is an added financial burden on producers and the high cost of insect control sometimes limits the areas in which cotton can be grown.

In 1970, the Committee on Genetic Vulnerability appointed by the National Academy of Sciences (1972) concluded that crop production in the USA was genetically vulnerable; our study has shown that genetic uniformity in cotton is greater today than 25 yr ago. A high degree of diversity within the germplasm has not translated to diversity in the field because only a few cultivars are extensively grown. If growers continue to plant a large portion of the hecterage to a single cultivar, genetic vulnerability will remain high. A greater utilization of the available germplasm by producers may reduce risks or costs associated with diseases and insect

pests; however, unless the diverse germplasm is equal in yield and other traits, the trend to greater uniformity will continue. Introgression of favorable alleles into a wider range of germplasm should be encouraged to ensure genetic diversity.

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