Genetic Uniformity of the U.S. Upland Cotton Crop since the Introduction of Transgenic Cottons

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ABSTRACT

Field genetic uniformity is the probability that any two plants selected at random within a region carry alleles that are identical by descent. Genetic uniformity of field crops can occur through breeding with genetically related backgrounds and grower choice of a few related cultivars among other factors. Transgenic cotton cultivars currently dominate the U.S. cottonseed market, comprising approximately 72% of the Year 2000 cotton hectares. All transgenic cotton cultivars were derived through backcross breeding with popular non-transgenic cultivars. The objective of this study was to apply pedigree analysis to estimate field genetic uniformity since transgenic cultivars were introduced into the U.S. cottonseed market in 1996. Coefficients of parentage and proportion of hectares planted to transgenic cultivars were employed to estimate field genetic uniformity for the southeastern, south-central, southwestern, and western production regions. Compared with field genetic uniformity estimated in the Year 1995 preceding introduction of transgenic cultivars, field genetic uniformity did change (0.18 vs. 0.13). The number of cultivars planted on the largest hectarage has not changed, but the percentage of the crop planted to a few cultivars has declined. The proportion of the hectarage planted to the most popular cultivar also has declined. Both of these factors affected field genetic uniformity resulting in a 28% reduction in uniformity across the USA.

FIELD GENETIC UNIFORMITY is the probability that any two plants selected at random within a region carry alleles that are identical by descent. Genetic uniformity predisposes crops produced over large hectarage to losses from biotic and abiotic stresses, an occurrence observed with the near failure of the southern corn (*Zea mays* L.) crop in 1970 (Ullstrup, 1972). Genetic uniformity of a crop can be enumerated by considering relationships among cultivars available for planting through molecular approaches or pedigree analysis. Pedigree analysis remains an attractive approach in cotton (*Gossypium hirsutum* L.) because of simplicity and the fact that most molecular markers exhibit low polymorphism within *G. hirsutum* (Paterson and Smith, 1999). Bowman et al. (1996) employed coefficients of parentage (r_p) to assess breadth of the cotton genetic base and found it to be relatively expansive, but that only a fraction of the available genetic base has been exploited in cultivar development. Van Esbroeck et al. (1998) calculated field uniformity (r_f) through 1995 considering cultivar genetic relationships adjusted for the hectarage planted to each cultivar. They found r_f to be relatively high (average $r_f = 0.30$) among the major cotton producing regions of the USA between 1970 and 1995, but increases in r_f because of the planting of genetically related cultivars was buffered by availability of new cultivars.

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Cotton cultivar development for certain U.S. production regions rested on a narrow genetic base in the early 1990s (May et al., 1995). Since 1995, the U.S. cotton crop has experienced a nearly complete turnover in major cultivars, primarily because transgenic cultivars possessing pest management traits have become very popular (USDA-AMS, 1996, 2000). Transgenic cultivars comprised 72% of U.S. hectarage in 2000. Cotton production has been simplified through the incorporation of a gene from *Bacillus thuringiensis* (Bt or Bollgard) imparting resistance to lepidopteran insect pests (Jenkins et al., 1997) and genes (Johnson, 1996) conferring resistance to application of the broad spectrum nonselective herbicide glyphosate [*N*-(phosphonomethyl)-glycine Roundup Ready, Monsanto Corp., St. Louis, MO, or RR], or the less broad spectrum herbicide bromoxynil (3,5-dibromo-4-hydroxybenzonitrile BXN). Many cultivars planted on significant hectarage since 1996 have either the herbicide tolerance gene alone or glyphosate with the Bt gene, and less frequently the Bt gene without an accompanying herbicide resistance gene. Cultivars containing the glyphosate resistance gene alone or in combination with a Bt gene comprised over 54% of the U.S. cottonseed market in 2000 (USDA-AMS, 2000).

Genetic uniformity of the U.S. cotton crop has not been determined since the deployment of transgenic cultivars. Backcross introgression (an average of three backcrosses) of pest management transgenes has been the most common method of cultivar development in recent years. All transgenic cultivars available to U.S. growers were derived through backcross breeding with genetically related recurrent parent cultivars widely grown in 1995. Genetic gains in lint yield may have suffered as a consequence. Genetic uniformity is further imposed through incorporation of the same transgenes into different genetic backgrounds because the DNA insert containing the transgene and its regulatory elements also is accompanied by DNA surrounding the site of insertion into the donor parent (Falconer, 1989), typically the cv. Coker 312. This nontarget DNA is not entirely eliminated during the introgression and selection phases of transgenic cultivar development. The objective of this study was to determine the impact of breeding transgenic cultivars on field genetic uniformity.

MATERIALS AND METHODS

Methods used in this study are identical to those published by Van Esbroeck et al. (1998). Data on hectarage planted for

Table 1. Percent hectarage of U.S. cotton planted with transgenic cotton cultivars since 1995 according to USDA-AMS.

Type†	1995	1996	1997	1998	1999	2000
	%					
BXN	<0.1	0.1	1.2	5.9	7.8	7.2
Bt	0	12.0	17.9	18.0	16.9	10.6
RR	0	0	3.1	17.1	24.2	10.8
Bt/RR	0	0	0.5	3.6	11.4	43.5
	–	–	–	–	–	–
Total	<0.1	12.1	22.7	44.6	60.3	72.1

† BXN = Buctril resistance; Bt = Bacillus thuringiensis; RR = glyphosate resistance.

the Year 2000 were gleaned from the USDA-AMS publication (USDA-AMS, 2000). The USDA-Agriculture Marketing Service furnished statistics on cotton planting for four production regions of the USA: Southeast, South-Central, Southwest, and West. Averages across regions may not be the same as the U.S. average because of the fact that the U.S. average is weighted by hectarage within regions, while averages across regions give equal weight to each region.

Analyses were performed only with cultivars that were planted on 1% or more of the hectarage within a region and across all regions. Both r_p and r_f were calculated. Bowman et al. (1997) described calculations and assumptions used in determining the coefficients of parentage. Cox et al. (1986) described the procedure used in determining field uniformity as the sum of all possible r values multiplied by the percentage of the hectarage grown in each cultivar. Higher r_p and r_f values are not desirable because genetic uniformity and vulnerability is increased and genetic diversity is decreased.

Where pedigrees of cultivars were unknown or unavailable (Calhoun et al., 1997), then an assumed r_p value of 0.07 between unknowns or between unknowns and knowns was used (Van Esbroeck et al., 1998). Only two cultivars had unknown pedigrees in the 2000 data set. Results from previous studies (Van Esbroeck et al., 1998) are reprinted by permission with additional data furnished by the authors.

RESULTS AND DISCUSSION

Growers rapidly adopted the new transgenic cottons first with the Bt cottons (Table 1). Tobacco budworm (*Heliothis virescens* F.) had developed resistance to synthetic pyrethroids and cotton could not be economically grown in certain areas, e.g., northern Alabama. The Bt cottons made cotton production economically profitable. Production of cotton cultivars with only the Bt gene declined in 2000 but the stacked version with glyphosate resistance was planted on over 43% of the hectarage. Glyphosate resistant cotton also was accepted readily with over 20% of the hectarage planted in the second year (1998) after becoming available, but declined in hectarage although the stacked version showed a dramatic increase in 2000.

Table 2. The number of cotton cultivars occupying at least 1% of the hectarage per region and across the USA at 5-yr intervals from 1970 to 2000.

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)
2000	19 (73)	17 (87)	15 (76)	15 (69)	26 (74)

† Number in brackets indicate the parentage of the total hectarage planted.

The percentage of the hectarage occupied by successful cultivars (defined as those occupying at least 1% of the hectarage within production regions and nationally) declined in 2000 in every region and across the USA (Table 2). Since 1995, the number of successful cultivars has remained relatively constant, suggesting that growers have planted a larger number of different cultivars than previously. In 1998, there were over 70 cultivars in the North Carolina Official Variety Trials (Bowman, 1998), whereas only 40 were tested in 1996 (Bowman, 1996).

In 2000, the South-central region was the most uniform region with a r_p of 0.29 (Table 3). The Southeast, which was the most genetically uniform region in 1995,

Table 3. Coefficient of parentage (r_p) among cotton cultivars occupying at least 1% of the hectarage in a region and across the USA at 5-yr intervals from 1970 to 2000.

Year	Region				Mean†	USA
	Southeast	South-central	Southwest	West		
1970	0.23	0.14	0.17	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
2000	0.28	0.29	0.19	0.15	0.23	0.17

† Arithmetic mean across regions.

Table 4. Field uniformity (r_f) for cotton growing regions across the USA at 5-yr intervals from 1970 to 2000.

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
2000	0.37	0.25	0.16	0.14	0.23	0.13

† Arithmetic mean across regions.

Table 5. Percentage of the hectarage occupied by the most widely grown cotton cultivar in a region and across the USA from 1970 to 2000.

	Region				
Year	Southeast	South-central	Southwest	West	USA
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
2000	13	16	25	20	9

became the second most uniform. The r_p in 2000 was higher across the USA (0.17) than the previous 25 yr and the mean of the four production regions (0.23) was the highest in this study. The mean for the USA was always lower than the mean across regions because the Southwest and West have a larger share of cotton production and the lowest r_p values of the four regions. The r_p value went up from 0.15 in 1995 to 0.19 in 2000 in the Southwest and remained the same in the West (Table 3).

Sixty-two percent of the successful cultivars grown in 2000 were developed by backcrossing transgenics into existing cultivars. Twelve of the 19 successful cultivars in the Southeast, 14 of 17 in the South-central, 9 of 15 in the Southwest, and 6 of 15 in the West resulted from backcrossing. The r_f values declined in every region except the Southeast and across all regions (Table 4). A dramatic reduction occurred in the South-central region where r_f went from 0.38 to 0.25. The most planted cultivar in that region was grown only on 16% of the hectarage (Table 5).

The Southwest region showed a slight reduction in field uniformity (Table 4). Two cultivars occupied half of the cotton hectarage in 1995 and 2000. However in 2000, the same two cultivars were the Roundup Ready versions. The region in the West also experienced a significant reduction in field uniformity (0.36 versus 0.14) (Table 4). Although the r_p value did not change from 1995 to 2000 (Table 3), hectarage occupied by the most grown cultivars changed (Table 5). Instead of one cultivar being planted on half the hectarage, the five most popular cultivars in 2000 only occupied 50% of the market.

Field uniformity across all regions averaged 0.23 in 2000, a reduction from 0.32 in 1995 (Table 4). This was a result of more cultivars planted on the same proportion of the hectarage. Overall the U.S. average field uniformity decreased from 0.18 in 1995 (the highest year in this study) to 0.13 in 2000, an improved direction (Table 4). The most popular cultivar across the belt only occupied 9% of the hectarage in 2000 (Table 5). The r_p value for the cotton belt in 2000 was the highest in this study (Table 3). However, the 26 successful cultivars only occupied 74% of the hectarage that year (Table 2).

As a group, the conventional cultivars were as related to all other cultivars as the transgenic cultivars (Table 6). The r_p means across regions and across the USA were nearly the same (0.23 versus 0.24 and 0.18 versus 0.17). Field uniformity would be expected to be higher for the transgenic cultivars because they were planted on 72.1% of the hectarage (Table 1). Thus, the r_f means across region and the USA (0.05 versus 0.18 and 0.03 versus 0.10) reflect the high field uniformity (Table 6).

The coefficient of parentage within groups differed only slightly when averaged across regions and USA (0.22 versus 0.19 and 0.11 versus 0.15) (Table 6). Large differences between groups were seen in the South-central, Southwest, and West regions. In the South-central region, only three conventional cultivars were grown on substantial hectarage in 2000, and were very closely related to each other (r_p = 0.52).

In the Southwest, half of the planted cultivars were conventional but were not as closely related to each other as the transgenics (0.08 versus 0.18) (Table 6). In the West five transgenic cultivars and two sets of two were very closely related giving a r_p twice the size of that for the 10 conventional cultivars (0.12 versus 0.06). Within the group, the transgenics are not much different from the conventional cultivars in being closely related (0.22 versus 0.19 for the means across regions and 0.11 versus 0.15 for the USA). Presently, the transgenic cultivars are not contributing more than conventional cultivars to field genetic uniformity.

In 1970, cotton cultivars were being developed by four major cotton seed companies outside the Plains of Texas—Coker Pedigreed Seed Co., Delta and Pine Land Company, McNair Seed Farms, and Stoneville Pedigreed Seed Company. In 2000, Aventis, PhytoGen, Garst/AgriPro, and Seed Source in addition to Deltapine and Stoneville Pedigreed Seed Company were developing cotton cultivars. The Coker and McNair Seed Companies were purchased in the 1970s and 1980s, respectively. California Planting Cotton Seed Distributors were developing cultivars for the San Joaquin Valley. O&A, Inc. and JaJo Genetics were conducting cultivar development and marketing their cultivars through other companies. Syngenta Seeds, Inc., started developing cotton cultivars for South Texas. Monsanto began its own field operations in Mississippi. United Agri Products had been developing cultivars as well. Since 1974, there has been a 625% increase in private breeding

Table 6. Coefficient of parentage (rp) of transgenic and conventional cotton cultivars within and with all cultivars for cotton growing regions and across the USA for 2000.

			Region					
Classification	Measure	Group	Southeast	South-central	Southwest	West	Mean†	USA
With all cultivars	r_p	Conventional	0.31	0.29	0.17	0.14	0.23	0.18
		Transgenic	0.28	0.29	0.21	0.16	0.24	0.17
	r_f	Conventional	0.03	0.03	0.05	0.10	0.05	0.03
		Transgenic	0.34	0.22	0.11	0.05	0.18	0.10
Within group	r_p	Conventional	0.23	0.52	0.08	0.06	0.22	0.11
		Transgenic	0.21	0.24	0.18	0.12	0.19	0.15

† Arithmetic means across regions.

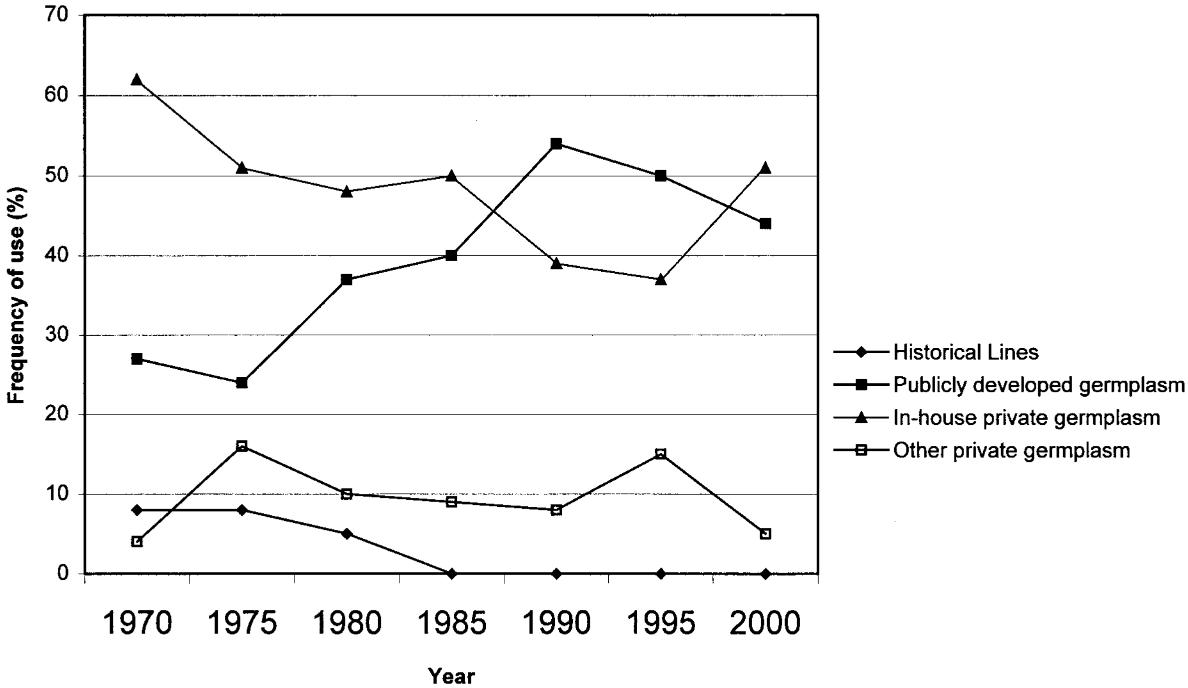

Fig. 1. Origin of parents used in the final cross for the development of cotton cultivars from 1970 to 2000.

efforts (Bowman, 1999). This massive increase in breeding efforts has temporarily negated the potential impact of a narrow germplasm base and also has served to fill the gap in current public breeding efforts.

In 1990 and 1995, public germplasm was the most common parental source in the final cross during the breeding of successful cultivars (Van Esbroeck et al., 1998). Before 1990 in-house private germplasm was the most common source (Fig. 1). By 2000, private germplasm had once again become the number one parental material in the final cross of successful cultivars primarily due to the use of backcrossing in the development of transgenic cotton cultivars. As mentioned previously, 62% of the successful cultivars in 2000 were developed in this manner. Private breeders spend 100% of their time on cultivar development, with 65% of that time spent on conventional breeding and the rest on transgenic breeding (Bowman, 2000). With this massive private breeding effort and the time spent on conventional breeding field uniformity should not increase in the near future. However, if breeders use the same few parents in their crossing programs to develop successful cultivars (Van Esbroeck et al., 1998), field uniformity could be seriously affected. Indeed, yield stagnation for the last 15 yr (Lewis, 2000) argues that efforts in the public breeding arena should not be diminished even with an increase in private breeding efforts.

REFERENCES

Bowman, D.T. 1996. North Carolina Measured Crop Performance: Cotton. N.C. Agric. Res. Serv. Crop Sci. Res. Rep. No. 163.

Bowman, D.T. 1998. North Carolina Measured Crop Performance: Cotton. N.C. Agric. Res. Serv. Crop Sci. Res. Rep. No. 176.

Bowman, D.T. 1999. Public cotton breeders- do we need them? J. Cotton Sci. 3:139–152.

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. 1996. Genetic base of upland cotton cultivars released between 1970 and 1990. Crop Sci. 36:577–581.

Bowman, D.T., O.L. May, and D.S. Calhoun. 1997. Coefficients of parentage for 260 cotton cultivars released between 1970 and 1990. USDA-ARS Tech. Bull. 1852. Govt. Print. Office, Washington, DC.

Calhoun, D.S., D.T. Bowman, and O.L. May. 1997. Pedigrees of upland and pima cotton cultivars released between 1970 and 1995. Miss. Agric. & Forestry Exp. Stn. Bull. 1069.

Cox, T.S., J.P. Murphy, and D.M. Rodgers. 1986. Changes in genetic diversity in the red and winter wheat regions of the United States. Proc. Natl. Acad. Sci. (USA) 83:5583–5586.

Falconer, D.S. 1989. Introduction to quantitative genetics. 3rd ed. John Wiley & Sons, New York.

Jenkins, J.N., J.C. McCarty, Jr., R.E. Buehler, J. Kiser, C. Williams, and T. Wofford. 1997. Resistance of cotton with Σ-endotoxin genes from *Bacillus thuringiensis* var. *kurstaki* on selected lepidopteran insects. Agron. J. 89:768–780.

Johnson, E.M. 1996. Roundup Ready™ gene in cotton. p. 51. *In* Proc. Beltwide Cotton Conf., Nashville, TN. 9–12 Jan. 1996. Natl. Cotton Counc. Am., Memphis, TN.

Lewis, H.L. 2000. Cotton yield and quality-yesterday, today, and tomorrow. p. 137–145. *In* C. Chewning (ed.) Proc. 13th Cotton Incorporated Engineered Fiber Selection System Conf., Raleigh, NC. 17–19 April 2000. Cotton Incorporated, Raleigh, NC.

May, O.L., D.T. Bowman, and D.S. Calhoun. 1995. Genetic diversity of U.S. Upland cotton cultivars released between 1980 and 1990. Crop Sci. 35:1570–1574.

Paterson, A.H., and R.H. Smith. 1999. Future horizons: Biotechnology for cotton improvement. p. 415–432. *In* C.W. Smith and J.T. Cothren (ed.) Cotton: Origin, history, technology, and production. John Wiley & Sons, New York.

Ullstrup, A.J. 1972. The impacts of the southern corn leaf blight epidemics of 1970–1971. Annu. Rev. Phytopathol. 10:37–50.

USDA-AMS. 1996. Cotton varieties planted–1996 Crop. USDA-AMS, Memphis, TN.

USDA-AMS. 2000. Cotton varieties planted–2000 Crop. USDA-AMS, Memphis, TN.

Van Esbroeck, G., D.T. Bowman, D.S. Calhoun, and O.L. May. 1998. Changes in genetic diversity of cotton in the U.S. from 1970 to 1995. Crop Sci. 38:33–37.