Effects of Plant Smoothness on Agronomic Traits of Upland Cotton—Lint Percentage¹

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ABSTRACT

In attempts to document agronomic deficits associated with plant smoothness in cotton (Gossypium hirsutum L.), two complete diallel sets involving various combinations of smoothness and pilosity alleles were grown in randomized, complete blocks at two locations in North Carolina in 1982. There were four replications per location. The first diallel was generated by intercrossing stocks homozygous for the allelic pairs Smil and smi, and Sm_2 and sm_2 , and the second from intercrossing Sm_2 and sm2, and Sm, and sm3. Increasing the number of Sm alleles increases plant smoothness, whereas the completely recessive genotype (all sm alleles) determines normally pubescent, the phenotype of 'Coker 310', the cultivar used as background. Within the two diallels, lint percentage varied from 38.1 to 43.3 with the lowest values associated with the Sm₂ allele, and the highest involving a hybrid of Sm_I^{tl} and sm_I . Although the Sm_I^{tl} allele was associated with a small deficit in lint percentage when homozygous, only the Sm₂ allele was accompanied by significant deficits, and that related to relatively low lint index. Number of seeds per boll, seed index (weight of 100 seeds, g), lint index (lint per 100 seeds, g), and grams of seed cotton per boll varied significantly among some entries. There was no evidence that values for any of these traits tracked degree of plant smoothness. Mostly additive effects were associated with significant contrasts for most of the traits, although there were some significant interaction effects, particularly with the Sm2 and sm2 pairs of alleles. There was no evidence that increasing plant smoothness to the point of eliminating trichomes reduced lint percentage any lower than that associated with the Sm₂ monomeric genotype.

Additional index words: Gossypium barbadense L., Gossypium hirsutum L., General effects, Specific effects, Maternal effects, Reciprocal effects, Plant pilosity, Lint index, Seed index, Genetic correlation.

THE pubescence of Gossypium hirsutum L., the species in which upland cotton is included, varies from dense to absent (6). Such variations in tomentum on plant surfaces has been of interest to cotton breeders because certain phenotypes confer resistance to specific insect pests (4, 5, 11, 12, 20, 23, 25), and ginned lint from the more glabrous phenotypes contain less foreign matter than that from hirsute cultivars (3, 10).

Four alleles at three independent loci imparting various levels of plant smoothness are now in advanced breeding lines, or are in cultivars. One such allele, Sm_1^{sl} , derives from, among other sources, G. barbadense L. (8). The allele, when homozygous and acting free of other smoothness alleles—the monomeric state, confines the trichomes on mature vegetative parts largely to the margins of leaves (6). The Sm_2 allele in the monomeric state imparts a phenotype similar to that of Sm_1^{sl} . Sm_2 was transferred to upland from the wild G. hirsutum accession WH-219, along with Sm_3 (6). The third allele in the monomeric

state limits trichomes to the principal leaf veins, leaf margins, petioles, and stems. The Delta Smooth allele, sm_3 , is recessive to the normally pubescent morph at the locus, sm_3^h , and imparts a phenotype similar to that of Sm_3 when the latter allele is in either the heterozygous or homozygous state. The Delta Smooth allele has been used widely in cotton breeding programs to reduce vegetative trash in ginned lint (3), and the allele seems to inflict no quality deficits.

Combining Sm_2 with either Sm_1^{sf} or Sm_3 in the dimeric state imparts ultra-smoothness, i. e., no trichomes appear on vegetative parts of mature plants. The normal alleles at the sites have been listed as sm_1 , sm_2 , and sm_3^h (6). These alleles, when combined in the homozygous state, impart the density of pubescence commonly noted in upland cottons. Although the density of pubescence on these cottons is variable (22), all that I have examined shared the common feature of having trichomes appear and persist on all stages of leaf-vein branching except the fifth, or terminal, stage (6).

Some workers have reported agronomic deficits associated with cottons smoother than the level imparted by sm_3 , the most frequent being a reduction in lint percentage and fiber yield (2, 7, 16, 21, 25). Some reports stated that the more glabrous cottons were more susceptible to certain insect pests even as such smooth cottons were more resistant to some others (16, 21).

In 1971 Lee (7) reviewed the progress of breeding efforts using glabrousness and concluded that the problems encountered with using increased plant smoothness could be overcome by continued selection. Twelve years later, cotton more glabrous than the Delta Smooth phenotype have not arrived to commercial acceptance. The lack of interest in such cottons probably stems from continuing deficits in productivity, conspicuous among which is a lag in the recovery of lint percentage. Deficits in lint percentage could be an inherent part of the expression of glabrousness. Lint fibers are modified trichomes, and the number of these on the seed coat might be reduced as the potential for the expression of glabrousness increases.

The objectives of the research I report herein were twofold: i) to assess the impact of various combinations of smoothness alleles on lint percentage and associated traits, and ii) to determine if any disturbances in lint percentage so noted related to grade of plant smoothness.

MATERIALS AND METHODS

The Sm_1^{s1} allele used in the study (symbolized herein as a₁) stems from the obsolete cultivar 'Coker 413'. The other two smoothness alleles, Sm_2 (b₁), and Sm_3 (c₁), as pointed out earlier (6), derive from the wild G. hirsutum accession, WH-219. The pilosity alleles, $sm_1(a_0)$, $sm_2(b_0)$, and $sm_2^h(c_0)$, were taken from 'Coker 310', an upland cultivar adapted

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Table 1. Means and Tukey's honestly significant differences for lint percentage and associated traits, Exp. 1.

Entry no.	Genotype	Lint percentage	Seed index	Lint index	Seed cotton per boll	Seeds per boll
		%		g		no.
1	$2(\mathbf{a}_1\mathbf{b}_0)$	41.1 bcde†	9.03 a	6.10 ab	6.23 bc	30.8 a
2	X a ₀ b,	41.3 bcd	9.20 a	6.35 a	6.55 abc	31.6 a
3	Xa,b	40.1 de	9.15 a	5.96 abc	6.81 a	33.8 a
4	X a ₀ b ₀	42.2 abc	9.04 a	$6.09~\mathrm{abc}$	6.48 abc	31.4 a
5	$2(\mathbf{a}_0\mathbf{b}_1)$	39.4 e	9.00 a	5.71 bc	6.49 abc	33.0 a
6	X a ₁ b ₀	40.7 cde	8.78 a	5.47 c	6.51 abc	34.1 a
7	Xa ₁ b ₁	39.9 de	9.49 a	6.00 abc	6.71 a	32.8 a
8	X a ₀ b ₀	41.3 bcd	8.76 a	5.98 abc	6.61 ab	34.5 a
9	2(a,b,)	39.4 e	9.22 a	5.68 bc	6.13 c	30.4 a
10	Xa,b	41.1 bcde	8.91 a	6.00 abc	6.54 abc	33.4 a
11	$X a_0 b_1$	39.8 de	9.45 a	6.05 abc	6.76 a	33.1 a
12	X a _o b _o	40.8 cde	8.86 a	5.78 bc	6.38 abc	32.6 a
13	$2(a_0b_0)$	42.5 ab	8.53 a	6.01 abc	6.16 bc	31.1 a
14	X a ₁ b ₀	43.3 a	9.00 a	6.48 a	6.53 abc	31.9 a
15	X a ₀ b ₁	41.4 bcd	8.68 a	6.05 abc	6.70 a	35.5 a
16	Xa ₁ b ₁	40.8 cde	9.00 a	5.68 bc	6.46 abc	32.9 a
	Tukey's HSD (0.05)	1.8	1.03	0.62	0.46	6.3

[†] Means followed by a common letter within the same column do not differ significantly at the 0.05 probability level.

for production in North Carolina and adjoining regions. An unknown number of generations of backcrossing and pedigree selection were used to transfer the smoothness alleles to upland background. Six additional backcrosses were used to transfer the genes to Coker 310. Each of the smoothness genes was sufficiently expressive in heterozygotes to allow for direct backcrossing without any intervening selection.

At the end of the sixth backcross, plants of the desired phenotypes were selected and selfed to produce the following monomeric genotypes: $a_1a_1b_0b_0c_0c_0$, $a_0a_0b_1b_1c_0c_0$, and $a_0a_0b_0b_0c_1c_1$. Six plants of each genotype were taken at random and crossed as follows: a_1a_1 monomeric X b_1b_1 monomeric, and b_1b_1 monomeric \times c_1c_1 monomeric. F_2 populations were grown from each cross, and the following genotypes were selected from the two families: family 1, $a_1a_1b_0b_0c_0c_0$, $a_0a_0b_1b_1c_0c_0$, $a_1a_1b_1b_1c_0c_0$, and $a_0a_0b_0b_0c_0c_0$, and in family 2, $a_0a_0b_1b_1c_0c_0$, $a_0a_0b_0b_0c_1c_1$, $a_0a_0b_1b_1c_1c_1$, and $a_0a_0b_0b_0c_0c_0$.

The monomerics in family 2 were readily separated by the pattern of trichomes on mature leaves, whereas progeny testing was required for distinguishing between a_1a_1 and b_1b_1 monomerics in family 1. The dimeric smooth segregates in the two families were equally glabrous, there being no trichomes on mature plant parts.

The genotypes selected for the two families were intercrossed in all possible combinations to provide seed for two 4 × 4 diallel sets. These were planted in 1982 at two locations in North Carolina in randomized, complete blocks with four replications per location. The plots were 8 m in length and were on 1-m centers. Soil at one location, the Upper Coastal Plains Research Station, Rocky Mount, was a Marlboro silt loam, (clayey, kaolinitic, thermic Typic Paleudults) and at the Central Crops Research Station, Clayton, a Dothan loamy sand (fine-loamy, siliceous, thermic Plinthic Paleudults). Standard cultural practices were used throughout the season.

Fifty well-opened bolls were picked at random from each plot at each location. The boll samples were subsampled for the estimation of number of seeds per boll, lint index, and seed index before ginning. The following traits were estimated: i) lint percentage—the fraction of the seed cot-

Table 2. Individual degrees of freedom comparisons for various traits in Exp. 1; Sm_1^{sl} vs. $sm_1 = a$, and Sm_2 vs. $sm_2 = b$.

	Mean squares for:			
Effect	Lint percentage	Seed cotton per boll	Seeds per boll	
General				
$\alpha_{\mathtt{a}}$	9.08**	0.00	37.51**	
$\alpha_{\mathbf{h}}$	68.08**	0.29*	17.02	
$(\alpha\alpha)_{ab}$	0.88	0.42*	6.25	
Specific				
$\delta_{\mathbf{a}}$	8.41**	0.02	2.00	
$\delta_{\mathbf{b}}^{\mathbf{c}}$	1.58	1.28**	98.00**	
$(\alpha/\alpha)_{ab}$	3.19	0.04	4.00	
$(\alpha \delta)_{ab}$	1.93	0.32*	0.02	
(αδ) _{ba}	1.89	0.01	1.27	
$(\delta\delta)_{ab}$	2.21	2.37**	47.53	
Maternal				
$\theta_{\mathbf{a}}$	2.85	0.11	8.27	
$\theta_{\rm b}^-$	0.77	0.07	0.77	
$(\theta\theta)_{ab}^{b}$	1.66	0.00	2.25	
Reciprocal				
$(\delta \theta)_{\mathbf{ab}}$	0.00	0.00	13.14	
$(\delta\theta)_{ba}$	0.29	0.06	6.89	
$(\delta\theta\theta)_{aab}$	2.21	0.01	0.06	
Error (90 df)	1.03	0.07	12.45	

^{*,**} Significant at the 0.05 and 0.01 levels, respectively.

ton that was lint, ii) lint index—grams of lint per 100 seeds, iii) seed index—weight of 100 fuzzy seeds in grams, iv) mean number of seeds per boll, and v) seed cotton per boll in grams.

The data were processed through ANOVA to secure error terms for the estimation of Tukey's honestly significantly differences, and the sums of squares for entries partitioned for individual degrees of freedom comparisons for general (additive), specific (dominance and epistasis), maternal, and reciprocal (maternal × embryonic) effects using methods developed by Cockerham [Lee et al. (9)] who also outlined the expectations for the effects.

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RESULTS AND DISCUSSION

Experiment 1

Means and Tukey's honestly significant differences among means for the various traits sampled in Exp. 1 are given in Table 1. The parental entries, 5 and 9, both homozygous for b_1 (Sm_2), displayed significantly lower lint percentage than entry 13, the normally pubescent control. Overall, 39% of the variance among entries for lint percentage was accounted for by pooling the four entries homozygous for b_1 and comparing them with the remainder of the array. Entry 1, homozygous for a_1 (Sm_2^{s1}), did not differ significantly from entry 13 in lint percentage. Still, the difference, 1.4%, might be regarded as important by modern breeders and growers of cotton.

There were no significant differences in seed index among the entries in Exp. 1. There were significant differences in lint index, but little evidence that lint index tracked level of plant smoothness. Overall, there was a significant correlation of 0.53 between lint index and lint percentage, and a significant correlation -0.42 between seed index and lint percentage.

There were significant differences among entries for grams of seed cotton per boll, but no indication that changes in the trait related to degree of plant smoothness. There were no significant differences

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Table 3. Means and Tukey's honestly significant differences for lint percentage and associated traits, Exp. 2.

Entry no.	Genotype	Lint percentage	Seed index	Lint index	Seed cotton per boll	Seeds per boll
		%		g		no.
1	$2(\mathbf{b}_1\mathbf{c}_0)$	38.1 e†	9.71 a	5.71 b	6.59 a	32.0 ab
2	X bocı	39.7 d	8.90 ab	5.81 ab	6.74 a	35.9 a
3	$X b_i c_i$	40.3 bcd	9.46 ab	6.03 ab	6.68 a	32.1 ab
4	X b ₀ c ₀	41.5 ab	8.95 ab	6.29 ab	6.43 ab	31.9 ab
5	$2(\mathbf{b}_0\mathbf{c}_1)$	40.7 abcd	9.48 ab	6.53 ab	6.51 ab	30.9 ab
6	X b ₁ c ₀	39.8 cd	9.54 ab	6.36 ab	6.74 a	33.0 ab
7	$X b_i c_i$	40.8 abcd	8.69 b	6.11 ab	6.48 ab	33.9 ab
8	X b₀c₀	41.5 ab	9.11 ab	6.19 ab	6.53 ab	32.3 ab
9	$2(b_1c_1)$	39.8 cd	9.01 ab	5.75 b	5.88 c	29.3 b
10	X b ₁ c ₀	40.6 abcd	8.91 ab	6.18 ab	6.71 a	34.9 a
11	$X b_0 c_1$	40.5 bcd	9.19 ab	6.05 ab	6.39 ab	31.5 ab
12	$X b_0 c_0$	42.1 a	8.79 b	6.16 ab	6.41 ab	32.5 ab
13	$2(b_0c_0)$	41.3 abc	8.68 b	5.90 ab	6.09 bc	30.9 ab
14	X b ₁ c ₀	40.3 bcd	9.21 ab	6.00 ab	6.49 ab	32.1 ab
15	X b₀c₁	41.4 ab	9,29 ab	6.30 ab	6.74 a	32.1 ab
16	$X b_1 c_1$	41.7 ab	8.85 ab	6.25 ab	6.41 ab	32.6 ab
	Tukey's HSD (0.05)	1.5	0.87	0.76	0.47	5.1

[†] Means followed by a common letter within the same column do not differ significantly at the 0.05 probability level.

among parents and hybrids for number of seeds per boll.

Individual degrees of freedom comparison for lint percentage, grams of seed cotton per boll, and number of seeds per boll are given in Table 2. There were significant additive effects for both the a and b pairs of alleles for lint percentage, and significant dominance effects for the a pair. The latter estimate resulted from the dominance of entry 13 in the two crosses with entry 1 (entries 4 and 14).

There was evidence for additive effects for the b pair of alleles for grams of seed cotton per boll, and a highly significant estimate of dominance for the b pair, largely because of a tendency for entries harboring the b_1 allele to produce large fruits. The significant additive \times additive effect is suspect, however, because the cis term (third from the top) is not matched by a significant trans term (sixth in the list). There was a highly significant dominance \times dominance interaction for grams of seed cotton per boll. Under number of seeds per boll, there was a highly significant dominance estimate for the b pair of alleles, perhaps related to the larger fruit size of entries harboring b_1 .

Experiment 2

Means and Tukey's honestly significant differences among means for the various traits sampled are given in Table 3. In Exp. 2 the reduction in lint percentage associated with the b_1 monomeric (entry 1) was even greater, when compared with the normally pubescent control (entry 13), than in Exp. 1. Although the remaining three genotypes homozygous for b_1 , entries 3,9, and 10, were significantly higher in lint percentage than entry 1, none were as high as the control. Pooling the four entries homozygous for b_1 and comparing these with the remainder of the array accounted for 32% of the variance among entries. Entry 5, the c_1 (Sm_3) monomeric, did not differ significantly from the control in lint percentage.

There were highly significant differences among entries for both seed index and lint index in Exp. 2, but little evidence that either related directly to level of plant smoothness. There was a significant correlation of 0.53 between lint index and lint percentage, and a significant correlation of -0.62 between seed index and lint percentage.

Meredith and Bridge (15) defined the relationship between lint index and seed index in cotton as lint index / (lint index + seed index) = lint percentage.Therefore, lint index and seed index are the component characters of lint percentage, and selection for increased lint percentage manipulates the two traits, often through reducing seed index while increasing the relative abundance of the lint on the seed (15). Therefore, the two traits have the greatest utility for comparative purposes when compared jointly. For example, in Exp. 2 entries 1 and 13 are similar in lint index but significantly various in lint percentage. In that particular comparison, the disparity in lint percentage seemed to relate to a striking difference in seed index. Entry 5, monomeric for c₁, was not significantly different from entry 13 in lint percentage, although seed index was somewhat greater. High lint percentage was seemingly maintained in entry 5 through an equal density of lint on a larger seed, the ratio of seed index to lint index being virtually the same for entries 5 and 13 at 1.00 and 1.01, whereas the ratio comparing entries 1 and 13 was 1.00 to 1.16. I therefore concluded that in Exp. 2 the b₁ monomeric was associated with increased seed size coupled with a decrease in the relative amount of lint on the seed. The relationship outlined above was not so striking in Exp. 1, but nonetheless present.

There was no significant correlation between lint index and seed index in either experiment, 0.14 in Exp. 1, and 0.06 in Exp. 2. The lack of correlation between seed index and lint index in these experiments amplifies the notion that the alleles chosen for use, or possibly germplasm linked with the genes, affect components of lint percentage in different ways. The similarity of seed size between entries 1 and 5 in Exp. 2, coupled with the disparity in lint index between the two entries, serves as a case in point.

Meredith and Bridge (15) found that increased number of seeds per boll in a Deltapine cultivar was accompanied by decreased seed index, which, in turn, led to increased lint percentage. In neither experiment was there evidence for correlation between the number of seeds per boll and lint percentage, -0.13 and -0.15 for Exp. 1 and 2 respectively. There were significant differences for number of seeds per boll in Exp. 2 but no evidence that changes in the trait tracked degree of plant smoothness. Only entry 9 was significantly various from the remainder of the entries for grams of seed cotton per boll.

Individual degrees of freedom comparisons for lint percentage, grams of seed cotton per boll, and number of seeds per boll are given in Table 4. Lint percentage in Exp. 2 was evidently transmitted in a more complex fashion than in Exp. 1. Only the b pair of alleles displayed significant additive effects. There was a large, highly significant, additive × additive effect, and evidence for some specific effects. In Table 3

Table 4. Individual degrees of freedom comparisons for various traits in Exp. 2; Sm_2 vs. $sm_2 = b$, and Sm_3 vs. $sm_3^h = c$.

	Mean squares for:			
Effect	Lint percentage	Seed cotton per boll	Seeds per boll	
General				
$\alpha_{\mathbf{b}}$	39.22**	0.00	12.25	
$\alpha_{\mathbf{c}}$	0.38	0.11	1.89	
$(\alpha\alpha)_{\mathbf{bc}}$	42.74**	2.81**	42.25*	
Specific				
$\delta_{ m b}$	3.61*	0.06	52.82*	
$\delta_{\mathbf{c}}$	8.15**	2.21*	67.57*	
$(\alpha/\alpha)_{bc}$	4.36*	0.25	1.00	
$(\alpha\delta)_{\mathbf{bc}}$	4.57	0.07	20.25	
$(\alpha\delta)_{ch}$	2.21	0.06	22.26	
$(\delta\delta)_{bc}$	6.62**	1.16**	5.64	
Maternal				
$\theta_{\mathbf{b}}$	1.38	0.02	0.02	
$\theta_{\mathbf{c}}$	0.95	0.04	2.25	
$(\theta\theta)_{\mathbf{bc}}$	1.69	0.05	3.52	
Reciprocal				
$(\delta\theta)_{bc}$	0.00	0.03	20.25	
$(\delta\theta)_{\mathrm{ch}}$	0.09	0.03	22.56	
$(\delta\theta\theta)_{\mathbf{bbc}}$	2.97	0.08	30.25	
Error (90 df)	0.72	0.07	8.30	

^{*,**} Significant at the 0.05 and 0.01 levels, respectively.

note that the entries that are doubly-heterozygous for smoothness alleles, nos. 2, 6, 12, and 16, did not match very well in lint percentage. In fact, there is a pronounced cis (entry 9×13) by trans (entry 1×13) 5) effect. The cis-trans difference accounted for most of the additive X additive interaction, but not all. A lesser contribution stemmed from the highly significant difference between entry 9 (dimeric smooth) and the b₁ monomeric. That result was interpreted to mean that the b₁ allele that became fixed in the dimeric smooth entry had released a block of germplasm during the process of transfer to Coker 310 and the selection of the parental stocks that related to increased seed size. Note that entry 9, while showing somewhat lower seed index than entry 1, still had about the same lint index. The resulting disequilibrium in the cis-trans heterozygotes seems to have spawned the kinds of interactions not usually noted in the transmission of lint percentage. Crosses of upland cotton in the past have rarely displayed other than additive effects for the trait (14, 15, 17, 18, 24).

Again, as in Exp. 1, the significant estimate for additive \times additive effects for grams of seed cotton per boll was suspect, and both the b and c pairs of alleles displayed dominance for the trait.

General Conclusions

The firmest conclusion drawn from the data was that in Coker 310 background the b_1 allele (Sm_2) , when homozygous, was associated with an unacceptable reduction in lint percentage, and that a_1 (Sm_1^{sl}) might not compete well with normally pubescent phenotypes of similar background in modern cotton breeding programs. Although Worley et al. (26) did not recognize lint percentage as a true component of fiber yield, the trait is treated as such by breeders and growers of cotton, and lint percentage, a trait readily manipulated by selection (15), correlates highly with fiber yield (1, 13, 19).

Still, I could find no evidence that changes in lint

percentage tracked degree of plant smoothness in any precise way. The ultra-smooth entries—no. 9 in both trials—did not display lint percentage below that of the b₁ monomeric in either experiment, and in Exp. 2 the lint percentage of entry 9 was significantly higher than that of entry 1, the b₁ monomeric. That result was interpreted to mean that the actual grade of smoothness was of less importance in determining lint percentage than the influence of certain of the alleles that imparted smoothness, or of germplasm linked with the genes.

The b₁ allele was associated with the greatest deviation in lint percentage when compared with the control entries, and that seems to have related mostly to the expression of relatively low lint index coupled with increased seed size. The data afforded no clue as to whether or not low lint index was attributable to linkage or pleiotropy, but did suggest linkage with germplasm that increased the size of the seeds of some entries homozygous for the by allele.

some entries homozygous for the b₁ allele.

The persistence of low lint percentage through many generations of backcrossing does suggest manifold effects for the b₁ allele, but no evidence for an accumulative effect when two smoothness alleles are fixed in the dimeric state. Therefore, if there are pleiotropic effects associated with smoothness in cotton, the effects apply to specific alleles and reach maximum expression when such alleles are in the monomeric state.

The Sm_1^{sl} gene would seem a better choice than Sm_2 in breeding programs where more glabrousness than that imparted by the Delta Smooth allele is desired. However, such gains might be obtained at the expense of a small loss in lint percentage which could project a slightly lowered fiber yield. Perhaps gain in grade from less leaf trash could offset such a deficit in the marketplace.

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