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Two New Alleles at the sm_1 Locus in Cotton[1]

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ABSTRACT

Two new alleles were sited at the sm_1 locus of tetraploid *Gossypium hirsutum* L., upland cotton. One allele, derived from the wild Hawaiian tetraploid species, *G.tomentosum* Nutt. ex Seem., removed all trichomes from stems and most of the trichomes from mature leaves. The allele is dominant to "normally pubescent", the phenotype of most cultivars of upland cotton. The second allele stems from the Peruvian diploid species, *G. raimondii* Ulbr. The allele greatly enhanced density of tomentum of the upland cultivar 'Empire,' is dominant to "normally pubescent," and masks the expression of Sm_2 (A subgenome glabrousness allele). The finding of an allele at the sm_1 locus that enhances the density of pubescence, taken along with three other alleles at the locus that remove varying amounts of pubescence from the cotton plant, suggests that the sm_1 locus of the D subgenome is the homoeologue of the sm_2, or h_1, locus of the A subgenome which bears an assortment of alleles that produce similar effects.

***Additional index words:** Gossypium armourianum Kearn, G. barbadense* **L.,** *G. hirsutum* **L.,** *G. raimondii* **Ulbr.,** *G. tomentosum* **Nutt. ex Seem., Plant glabrousness, Trichomes.**

ALLELES at three loci remove pubescence from vegetative parts of plants of various species of *Gossypium* (4,5,6). An undetermined number of alleles regulate the density of pubescence on plants lacking smoothness genes (4). Recently Endrizzi and Ramsay (1), using telosomic cytogenetic techniques, placed the pubescence-enhancing genes of Knight (3), H_1 and H_2, and the plant smoothness allele of Lee (4), Sm_2, in the long arm of chromosome 6 of the A subgenome of *Gossypium hirsutum* L., upland cotton. Moreover, genetical tests showed that the three genes segregated as alleles when mated inter se.

The phenotypes bestowed by H_1, and H_2, and Sm_2 contrast sharply. The H alleles increase the density of pubescence greatly, whereas Sm_2, when homozygous, confines trichomes on mature vegetative parts largely to the margins of leaves. The work of Endrizzi and Ramsay is the first report of a precise genetical relationship between alleles of *Gossypium* that increase and decrease density of pubescence when the "normally pubescent" phenotype noted in most upland cottons is used as the standard of comparison.

Recently, two new alleles have come to light, one enhancing pubescence, and the other curtailing the development of such vestiture. The objectives of the current study were: i) to determine the allelic relationships of the new genes, and ii) to compare the expression of the alleles in an Upland background to other alleles that alter plant pilosity.

MATERIALS AND METHODS

The allele that decreases plant pilosity was derived from the Hawaiian wild tetraploid species, *G. tomentosum* Nutt. ex Seem. Knight (3) showed that the short, dense tomentum of the Hawaiian cotton was imparted by the allele H_2 acting in the homozygous state. During the process of transfer of H_2 from the wild species to the upland cultivar 'Empire', I noted that a few backcross segregates had glabrous stems. Neither Empire nor *G. tomentosum* display glabrous stems, so I concluded that the character was latent in the Hawaiian cotton, its expression being hypostatic to H_2. That conclusion was based upon the finding of Ramey (7) that the Pilose

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allele, the *G. hirsutum* morph of H_2, was epistatic to Meyer's (6) D_2 Smooth allele, the *G. armourianum* Kearn. morph of Sm_1^{sl}, an allele with an expression similar to that of Sm_2.

Three such smooth-stemmed plants were saved and backcrossed to Empire. The ensuing generation displayed approximately equal numbers of plants with glabrous and pubescent stems. After two additional generations of backcrossing, four smooth-stemmed plants of good vigor were saved and selfed. The combined progenies of these segregated approximately one-fourth "normally pubescent" like Empire, one-half displayed glabrous stems and pubescent leaves, and one-fourth had glabrous stems and partially glabrous leaves.

Plants of the third class—a true-breeding group—were crossed with Z-106, a "normally pubescent" stock of the genotype $sm_1sm_1sm_2sm_2$, with 'Coker 413', a cultivar of the genotype $Sm_1^{sl}Sm_1^{sl}sm_2sm_2$, and with North Carolina Smooth 2, an experimental stock of the genotype $sm_1sm_1Sm_2Sm_2$, the Sm_2 allele residing in the A subgenome of tetraploid cottons.

AG-168-7, the stock with increased pubescence, was furnished by John Endrizzi of the Department of Plant Sciences, University of Arizona, Tucson. The strain was selected from plants of Empire that had been introgressed with germplasm from the Peruvian diploid species *G. raimondii* Ulbr., a wild cotton of the D genome group. Five greenhouse-grown plants of AG-168-7 averaged 18.2 ± 0.3 trichomes along a 1-cm transect taken from the abaxial surfaces of mature leaves, whereas seven plants of Empire from the same bench averaged 10.0 ± 0.4 trichomes per 1-cm transect. The density of pubescence of Empire grades in the upper range of cottons I describe as being "normally pubescent".

Bearing in mind that Endrizzi and Ramsay (1) showed that H_1, H_2, and Sm_2 were alleles at a common locus in the A subgenome of *G. hirsutum*, a reasonable hypothesis was that AG-168-7 bore a tomentum-enhancing allele at the sm_1 locus of the D subgenome, inasmuch as the increased tomentum of AG-168-7 derived from the D genome species, *G. raimondii*. Accordingly, I crossed AG-168-7 with Coker 413, the line homozygous for Sm_1^{sl}, to test for allelism, and with 'Coker 304', a cultivar that is homozygous for sm_1 and sm_2. Finally, I crossed AG-168-7 with North Carolina Smooth 2, although there was virtually no liklihood that any pubescence alleles of AG-168-7 could be allelic with Sm_2. The last cross was made to test the possibility that the determiner(s) of *G. raimondii* pubescence might be epistatic to Sm_2.

F_2 progenies were grown under field culture at the Central Crops Research Station, Clayton, NC on Dothan Sandy Loam, a member of the fine-loamy, siliceous, thermic Plinthic Paleudults. The progenies were scored at maturity for grade of pubescence on leaves and stems, and the results are presented in Tables 1 and 2.

RESULTS AND DISCUSSION

As shown in Table 1, the F_2 from the cross of *G. tomentosum Sm* × Z-106 did not fit the 3 to 1 segregation ratio expected. Still, observations on the progress of smoothness through the backcross generations used in transferring the phenotype to Empire, coupled with the sharp contrast between the phenotypes recorded in the BC and F_2 generations, left little doubt that the smoothness imparted was conditioned by a single, dominant allele. Moreover, the F_2 from the cross with Coker 413 did not show segregation, and the cross with North Carolina Smooth 2, the stock homozygous for the Sm_2 allele, gave a reasonable fit to 15 (with at least the stems smooth) to 1 ("normally pubescent"). Therefore, there seemed to be little doubt that *G. tomentosum Sm* was allelic with Sm_1^{sl} and was thus still another allele at the sm_1 locus of the D subgenome of the tetraploid cottons.

Viewed a priori, the finding of a glabrousness allele in the extremely pubescent *G. tomentosum* would seem unlikely, but there is a precedent for such an event. The group of *G. barbadense* cultivars known as the 'Tanguis' cottons are about as pubescent on vegetative parts as *G. tomentosum*. Knight (3) reported that Tanguis harbored H_1, which, in the interpretation of Endrizzi and Ramsay (1), is one of two alleles at the same locus in the A subgenome that impart dense pubescence. The pubescence of Tanguis cottons resembles that of T611, the stock of *G. hirsutum* that harbors Simpson's (9) H_2 allele, more closely than that of MU8b, Knight's (3) classical source of H_1.

Like *G. tomentosum*, Tanguis cottons harbor a smooth-stem allele, Sm_1^{sl} in the nomenclature of Lee (4, 5). Empire introgressed with Tanguis yielded plants with smooth stems and nearly smooth leaves, and the F_2 from a cross of Tanguis and a stock of Pima (*G. barbadense*), in which the sm_1 (pubescent stem) allele of *G. hirsutum* had been substituted for Sm_1^{sl}, yielded some smooth-stemmed plants that proved to be homozygous for Sm_1^{sl}. That bit of evidence, combined with the data presented herein, tends to sup-

Table 1. Allelism tests for the smoothness allele of *G. tomentosum*.

Gossypium crosses and generation	Phenotypes recovered: Smooth stem	Pubescent stem	Ratio proposed and p of fit
G. tomentosum Sm × Z-106, $sm_1sm_1sm_2sm_2$, F_2	156	32	3:1; 0.01–0.02
G. tomentosum Sm × Coker 413, $Sm_1^{sl}Sm_1^{sl}sm_2sm_2$, F_2	56	0	
G. tomentosum Sm × N.C. Smooth 2, $sm_1sm_1Sm_2Sm_2$, F_2	154	12	15:1; 0.50–0.75

Table 2. Allelism tests for pubescence-enhancing allele of AG-168-7.

Gossypium crosses and generation	Phenotypes recovered: Smooth stem	Increased tomentum	"Normally pubescent"	Ratio proposed and p of fit
AG-168-7 × Coker 304, $sm_1sm_1sm_2sm_2$, F_2	0	66	19	3:1; 0.50–0.75
AG-168-7 × N.C. Smooth 2, $sm_1sm_1Sm_2Sm_2$, F_2	72	(198) Intergradation essential	complete	†3:13; < 0.01 5:11; 0.10–0.25
AG-168-7 × Coker 413, $Sm_1^{sl}Sm_1^{sl}sm_2sm_2$, F_2	171	51	0	3:1; 0.25–0.50

† A ratio of 3:13 assumes full epistasis for the pubescence allele of AG-168-7; 5:11 assumes modified epistasis, i.e., one dose of the pubescence allele not epistatic to Sm_2Sm_2.

port Harland's (2) conclusion that *G. tomentosum* is more closely related to *G. barbadense* than to *G. hirsutum*. Moreover, the tomentum allele of Tanguis seems to be more closely related to H_2 than to H_1, inasmuch as the allele masks the expression of Sm_1^{sl} whereas Ramey (7) showed that H_1 does not.

The F_2 of the cross between Coker 304 and AG-168-7 graded roughly 3 densely pubescent to 1 "normally pubescent". A few segregates could not be placed with precision in one class or the other, but most assorted as documented in Table 2. Moreover, there was no evidence of transgressive segregation for density of pubescence in the F_2 population. Thus, the dense pubescence of AG-168-7 seemed to assort as a single character difference.

Inasmuch as *G. raimondii* is a D genome species of *Gossypium*, there was virtually no reason to believe that germplasm contributed to the tetraploid *G. hirsutum* from the wild diploid would be allelic with any genetic characters in the A subgenome of the tetraploid species. Nevertheless, AG-168-7 was crossed with North Carolina Smooth 2 to observe the relationship between the pubescence of *G. raimondii* and the Sm_2 allele. The leaves of the F_1 showed about the same density of pubescence as Coker 304, and the stems were pubescent, but not as tomentose as those of AG-168-7. Therefore, there was evidence that *G. raimondii* tomentose was epistatic to Sm_2.

The F_2 displayed more smooth-stemmed plants than expected when the tomentum of AG-168-7 was assumed to be epistatic to Sm_2, and the tomentose group showed essentially a complete range of pubescence density between Coker 304 and AG-168-7.

The F1 of the cross of Coker 413 with AG-168-7 displayed smooth stems and tomentose leaves, the tomentum being of a reduced grade. The F_2 segregated approximately three plants with smooth stems to one with hairy stem. There was evidence that the smooth stem class could have been subdivided into two groups, tomentose and smooth leaf, but that was not done. Twenty random plants of the hairy-stemmed class averaged 17.8 ± 0.4 trichomes per 1 cm transect of abaxial leaf surface, whereas 30 plants of Coker 304 from a nearby row averaged 7.3 ± 0.4 trichomes per 1 cm transect. Therefore, the density of tomentum of AG-168-7 was transmitted as a unit when mated with Sm_1^{sl}, and thus behaved as an allele of Sm_1^{sl}.

The finding that the tomentum unit of AG-168-7 assorted as an allele at the sm_1 locus very likely relates to the work of Saunders (8) who transferred a tomentum allele from *G. raimondii* into the *G. hirsutum* var. *punctatum* stock, T.S.2. In the new background the allele was designated H_6.

T.S.2, like various other "ultra-smooth" race stocks of *G. hirsutum*, proved, after analysis at Raleigh, to be homozygous for Sm_2. Therefore, when Saunders used the hexaploid bridging technique to transfer H_6 to T.S.2, the tomentose stock recovered as a tetraploid must have been homozygous for Sm_2. Earlier in this report I presented evidence that the AG-168-7 tomentum allele was epistatic to Sm_2. Still, I do not know whether one dose of the allele, presumably H_6, is epistatic to two doses of Sm_2. The results from scoring the F_2 in Table 2 suggests that two doses of H_6 are required to mask the smoothness potential of stocks homozygous for Sm_2.

I shall not propose any symbols for the two new alleles considered herein. A full-scale revision of the genetical nomenclature for the hairiness-smoothness system for *Gossypium* is planned, and the *G. tomentosum* smoothness and the *G. raimondii* tomentum alleles will be dealt with in that report.

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