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Glabrous-Stem Inheritance in Upland Cotton[1]

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UPLAND cotton *(Gossypium hirutum* L.) has hirsute leaves and stems according to Smith (13), who counted trichomes on plant parts of cultivars that were then in use in the U.S.A. A "smooth leaf" cultivar had fewest leaf trichomes and the hirsute cultivars had 4 to 40 times as many. Trichome numbers on petioles and leaves were highly correlated; the "smooth-leaf" type had 7 trichomes per 6 mm of petiole and the hirsute cultivars had 2 to 7 times as many. His glabrous experimental having *SmSm,* smooth stem, had 0 trichomes on the stem and petiole and fewest leaf trichomes. In comparison, pilose experimentals having *H2H2*, pilose leaves, stems, and bolls, had several times as many trichomes on all plant parts as the hirsute cultivars according to Saunders' (8) figure and observations (8, 9, 10).

In the Rio Grande Valley of Texas, oviposition of two *Heliothis* species (the cotton bollworm) was related to leaf and stem hairiness of most cultivars (writer's unpublished data). Pilose experimentals in 1961 had significantly more *Heliothis* eggs per plant than hirsuite cultivars and hirsute types had more than glabrous-stem experimentals, but the stocks having *Sm* were not investigated. The two *Heliothis* species oviposited more eggs on pilose than hirsute and more on hirsute than smooth experimentals having *SmSm* in 1962. Again in 1963, the two species placed most eggs on hirsute and fewest on glabrous-stem experimentals which had various smooth-stem genes. The "smooth-leaf" cultivars were intermediate between the two types. Based on this experience, the development of glabrous-stem cultivars should be a step toward resistance against the *Heliothis* complex, which is becoming increasingly difficult to control across the cotton belt. This paper is concerned with inheritance of stem hair in five glabrous-stem sources and the relationship among genes from these sources.

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REVIEW OF LITERATURE

Saunders (8) reviewed the development of hairy cultivars necessary in African environments for control of jassid insects. Breeders there used the well known *H1* gene, transferring it from several *G. hirsutum* varieties and related *Gossypium species.* He reinvestigated F_2 and F_3 populations of a glabrous T.S. 2 stock (hybridized with 3 highly hairy and 1 glabrescent cultivars) and reported that: *(1)* lower leaf laminal and stem and petiolar hair were highly correlated, as Smith (13) reported for the less hairy cultivars of the U.S.; *(2)* hair was initiated and increased in density only if H1 were present, except that in certain genotypes hair was prohibited although *H1* was homozygous; *(3)* pilose of American Upland T611 (gene *H2*) was a more reliable gene for producing a high density of hair but was less flexible than *H1* and its complex of modifying genes; *(4)* glabrous T.S.2 lacked *H1* but enhanced hair densities in the genotypes having *H1*; and *(5)* recovered glabrous plants bred true.

For *G. barbadense* L., which is generally glabrous, Saunders (9) showed that *H3* produced stem hair only if *H1* (from *G. hirsutum)* were present. The F_2 of glabrous-stem *barbadense* (*H1H1h3h3*) × glabrous T.S.2 had high grade stem and leaf hair in a small fraction of the plants, e.g., those which were *H1H1H3H3* where both *H1* and *H3* were obtained from *G. hirsutum.* He (10) transferred two genes for stem hair from hairy diploid *G. anomalum* Wawra. and Peyrs. and showed that these were alleles of *H1* and *H3* respectively.

Ramey (7) reported that *H1* and *H2* differed in the production of stem hair when each had been combined with *Sm,* smooth stem, in *G. hirsutum.* His *H1H1SmSm* had hairy terminals and smooth stem,s resembling *H1H1h3h3* of (9, 10) but *H2H2 SmSm* and *H2H2h1h1 h3h3* (of (9) in *barbadense)* had highest grade stem and leaf hair.

Phillips (6) reported *H*1 segregated at a high frequency in hexaploid *G. barbadense* × *G. arboreum* L., genome formula $2A_bD_bA_2$, and *Sm* segregated at a low frequency in hexaploid *G. hirsutum* × *G. armourianum* Kearney, $2A_hD_hD_2$. He did not report segregation of glabrous stem in his hexaploid *G. hirsutum* × *G. thurberi* Tod., $2A_hD_hD_1$, when he reported other D_1 segregation information. He indicated that segregation in hexaploids had placed *H*2 on the A subgenome of the amphidiploids. Endrizzi (1), using a monosomic, located *H*2 in the proximal end of the long arm of chromosome 6, an A subgenome chromosome. Saunders (10) reasoned that *H*1 and *H*3 were A subgenome gene substitutions from *G. anomalum*, $2B_1$, knowing that Knight (4) had obtained *H*1 from *G. herbaceum* L., $2A_1$, and that these two diploids had similar homeologues.

MATERIALS AND METHODS

The following stocks had glabrous stems:

G. hirsutum:
- T8Sm, an Austin gland-free version having *SmSm*
- CS41235, an experimental of the Coker Pedigreed Seed Company
- Socorro Island, a wild relic described by Fryxell and Moran (2)

G. barbadense:
- 21B1–1, a Pima experimental
- St. Vincent V135, a Sea Island of St. Vincent adaptation

G. thurberi:
- Raleigh collection

These stocks had hirsute stems:

G. hirsutum:
- T2, the gland-free, nectary-free version of T8Sm
- R293, a partially nectary-free having smsm genotype, as T2

The method was to hybridize each glabrous stock with hirsute T2 and to demonstrate the frequency of hirsute stem in F_2 and backcross to T2. (R293 had to be used with glabrous Socorro Island). To demonstrate relationship the glabrous stocks, except when stated otherwise, were crossed with T8Sm. Each F_1 was self-pollinated and testcrossed to T2.

Plants were observed at first flowering, green-boll, and openboll stages. Hair was occasionally not noticeable at first flower and open boll stages but was discernible at the green-boll stage. The discontinuity between glabrous and hirsute stem was generally greater than less than 1 trichome per standard stem length for *Sm* to more than 4 for *smsm*, as Smith (11) reported. As Saunders (8, 9, 10) observed, glabrous-stem in *hirsutum* was generally associated with a minimum of leaf hair. Some plants classed as glabrous-stem had discernible leaf hair in populations having Socorro Island and *G. thuirberi* parentage. *Heliothis* moths were ubiquitous at first flower and green boll stages and egg counts were related to leaf and stem-hair densities. A paucity of eggs was typical of glabrous-stem and an abundance of eggs was typical of hirsute-stem plants.

RESULTS AND EXPLANATIONS

T8Sm glabrousness. The *Sm* gene was easily detected in both F_2 and backcross populations of T2 parentage. In the small F_2 of Table 1 *Sm* segregation fitted a ratio of 3 glabrous to 1 hirsute for the 1964 season when most of the following populations were observed.

CS41255 glabrousness. A dominant gene for glabrousness was readily detected in both F_2 and backcross populations of CS41235 × T2. Segregation in Table 1 was in the ratio of 3 glabrous to 1 hirsute for the F_2. Recovered *smsm plants* had a high level of hours on stems and lower leaf lamina, which indicated simple inheritance in CS41235.

Only glabrous-stem plants occurred in F_2 (T8Sm × CS41235). The testcross, F_1 (T8Sm × CS41235) × T2, had only glabrous plants. A separation of glabrous-stem plants in each population could not be made according to parentage. The dominant genes of the two glabrous stocks were allelic.

Table 1. Segregation of stem hair in F_2 and backcross populations involving T2 and T8Sm and three glabrous stocks.

Parentage	Population	Plants with		P	
		Glabrous	Hirsute	3:1 in F_2	1:1 in TC
F_1 ($T8S_m$ × T2)	F_2	87	18	.07	
F_1 (CS41235 × T2)	F_2	38	10	.50	
F_1 (CS41235 × $T8S_m$)	F_2	29	0		
F_1 (CS41235 × $T8S_m$) × T2	BC	21	0	.01	
F_1 (21B1-1 × T2) × T2	BC	25	30		.50
F_1 (21B1-1 × $T8S_m$) × T2	BC	28	0	.01	
F_1 (R293 × Socorro Island)	F_2	31	5	.15	
F_1 × T2	TC	16	19		.50
T_2 × F_1	TC	19	15		.50
19 glabrous TC plants	TCF_2	192	85	.03	
11 hirsute TC plants	TCF_2	0	131		
4 hirsute TC plants	TCF_2	7	100		
(T2 × F_1) glabrous × T2	BC	8	11		.50
8 glabrous BC plants	BCF_2	114	49	.15	
11 hirsute BC plants	BCF_2	0	239		
(T2 × F_1) hirsute × T2	BC	0	8		
8 hirsute BC plants	BCF_2	2	245		
(T2 × F_1) glabrous × $T8S_m$	TC	8	0		
1 glabrous TC plant	TCF_2	35	(4?)	.01	
2 glabrous TC plant	TCF_2	33	0	.01	

(?) Atypical probably belonging in glabrous class.

G. barbadense glabrousness. A few intergraded plants usually associated with a tardy sluffing off of stem hair occurred in backcross F_1 (21B1–1 × T2) × T2. The plants with persistent stem-hair were retained in the hirsute class. As approximately equal numbers of plants were observed in each class, a dominant gene for glabrousness was indicated for 21B1–1.

In the backcross F_1 (21B1–1 × T8Sm) × T2, only glabrous-stem plants were observed. A tardy sluffing off of hair was observed in one population. Its 16 plants were grown and self-pollinated in a greenhouse and each F_2 produced hirsute-stem plants at a high frequency. The presence of a single *Sm* locus having allelic dominant genes was confirmed.

Socorro Island glabrousness. Plants of Socorro Island flowered infrequently and retained fruiting forms poorly, even during short-day lengths. Few flowers produced pollen. Three years elapsed before Socorro Island stock could be hybridized with T2 and T8Sm. In the meantime, the first hybrid obtained, F_1 (R293 × Socorro Island), was useful. It had glabrous stem and many other dominant characteristics of Socorro Island, such as short-day flowering, five seed per locule, and dormant seed. Nongerminating dormant seed depleted the first season's planting of F_2 and testcross to T2 as pollen parent. The remnant populations were further reduced in size by nonflowering.

The second season, to render seed coats permeable, seed were chipped. Nongerminability was not altered much. Germination was not improved much by hot water treatment at 170° F. for 2 minutes, as found helpful for "hard" cotton seed. The classification in Table 1 therefore was obtained from a smaller than anticipated set of F_2, testcross, testcross F_2, and first backcross to T2 F_2.

The small F_2 (R293 × Soc. I.) segregated five hirsute-stem plants. The testcross had a ratio of 1 glabrous to 1 hirsute. An out of season planting of a testcross (to T2 as seed parent to avoid maternally inherited "hard" seed) had 19 glabrous and 15 hirsute plants and repeated the 1:1 ratio of the preceding test-cross. Self-pollination of the plants produced 19 F_2 families from glabrous-stem parents, which contained some hirsute plants in F_2 although a few had more hirsute than glabrous plants. From hirsute parents 11 families contained only hirsute-stem progeny and 4 families had approximately 1/16 glabrous-stem plants.

The ratio expected from smooth testcross plants, based on the single gene segregation in the testcross, was 3:1 for the F_2. The observed segregation deviated from this ratio and the hirsute class was in excess of the expected frequency. A tardy sluffing off of hair was associated with plants classed as glabrous. Also, a tendency for hairy terminals and leaf lamina in some glabrous plants could lead to misclassification and an excess of hirsute-stem plants. Because the frequency of hirsute stem would have been smaller than the observed frequency if either 2 dominant *Sm* genes or 1 *Sm* and a recessive gene for glabrousness had been present, faulty classification of some hirsute plants was conceded.

The evidence for recessive genes for glabrous stem, as indicated by four families from hirsute parents, had been offset by troublesome characteristics of Socorro Island, which rendered the obtaining of large F_2 populations uneconomical.

A single testcross plant having glabrous stem was backcrossed to T_2 and the progeny was planted out of season. The expected ratio of 1 glabrous to 1 hirsute was obtained. Self-pollination and field sowing produced 8 families segregating in a ratio of 3 glabrous to 1 hirsute and 11 families segregating for Socorro Island characteristics but homozygous for hirsuteness. A single dominant gene for glabrousness had been present in the parental glabrous plant. Similarly, a hirsute testcross plant was backcrossed to T2 and the offspring self-pollinated. Two intergrade plants (classed as glabrous) and the remaining hirsute plants were observed. The hirsute parental plant was quite similar to hirsute Upland stocks in breeding behavior.

Another glabrous plant of testcross F_1 (R293 $\times$ Soc. I) $\times$ T2 was hybridized with T8Sm for testcrossing. Plants of this testcross were self-pollinated and the seed were field sown. Two glabrous testcross plants deviated from the other 6 glabrous by failing to segregate in a ratio of three to one. These two, at the bottom of Table 1, seemed to be segregating for *Sm* of T8Sm and an allele for tardy sluffing off of stem hair, since 4 atypical glabrous-stem plants had hairy terminals and hirsute stems until open-boll stage. However the presence of stem hair might have been caused by recombination of *H3H3*, or its allele, from Socorro Island with *SmSm*. Stem hair was produced in Saunders' (10) glabrous $\times$ glabrous F_2.

G. thurberi glabrousness. Diploid *G. thurberi* was manipulated from synthetic amphiploid *G. arboreum-G. thurberi* $2A_2D_1$. In this amphiploid, genes for hairiness (*H*1, etc.) of $2A_2$ interacting with genes for glabrousness of $2D_1$ produced a small amount of closely appressed stem hair. The F_1 ($2A_2D_1 \times$ T2) had more stem hair than the synthetic and was a genuine between grade, as compared with *Smsm* glabrous and *smsm* of *hirsutum*. Like another trispecies the writer studied, $A_2D_2A_hD_h$, which had the single *Sm* gene of $2D_2$ (and T8Sm), F_1 ($2A_2D_1 \times$ T2) had a single *Sm* gene. This *Sm* gene was easily manipulated by (1) replacing it with a gene for hirsuteness from *hairy* diploid *G. raimondii* Ulbr. $2D_5$, (2) testing it against *Sm* allele of *G. barbadense* St. Vincent, and (3) testing it against the *Sm* alleles of St. Vincent and CS41235. In procedures (2) and (3) interfering A subgenome genes (*H*1, *H*3, and (?)*H*2) would enhance the frequency of occurrence of hirsute stem in testcrosses with T2, since together *H*1 and *H*3 produced hairy stem for Saunders (9, 10) and *H*2 and *Sm* made hairy stem for Saunders (10) and Ramey (7).

1. Replacement of Sm of G. thurberi. Amphidiploid F_1 ($2A_2D_1 \times 2A_2D_5$) was obtained by crossing synthetic $2A_2D_1$ with synthetic *G. arboreum-G. raimondii* ($2A_2D_5$). It was highly infertile (for causes other than lack of chromosome homology) but was eventually backcrossed using pollen of $2A_2D_1$. Two backcross plants were obtained; one was a glabrous-stem dwarf and the second a low grade hirsute that had a number of D_5 marker genes. The second when testcrossed with T2 produced two vigorous plants. The backcross of each to T2 (Table 2) shows that *Sm* of *G. thurberi* was present in one testcross plant and had been replaced by a gene for hirsute stem from *G. raimondii* in the other.

2. Testing Sm of G. thurberi against Sm of G. barbadense. Glabrous F_1 ($2A_2D_1 \times$ St. Vincent) was testcrossed with T2 and either weakly hirsute or glabrous-stem plants were obtained. Three of the hirsute plants were self-pollinated and collectively produced both glabrous and hirsute-stem plants. In the hirsute class, hairy plants having high grade stem and leaf hair were observed in addition to the hirsute plants. One or more modifiers for hair had been transferred from the A subgenome, but glabrousness had been masked in the parental testcross plants. One glabrous testcross plant when self-pollinated produced only glabrous-stem offspring; when backcrossed to T2 it produced both glabrous and hirsute classes. These data suggest that in certain genotypes heterozygous *Smsm* produced a hirsute phenotype. At first glance the masked *Sm* gene seemed to be from *G. thurberi*.

3. Testing Sm of G. thurberi and G. barbadense against CS41235. As reported in the 3rd grouping of Table 2, F_1 ($2A_2D_1 \times$ St. Vincent) was outcrossed to CS41235. Eight of 12 glabrous outcross plants were testcrossed with T2 (although each of the 12 was self-pollinated). The testcrosses were useful but the 12 outcross F_2 families varied so drastically in plant vigor that classification was of little value. Five of 8 testcrosses segregated for equal fractions of glabrous and hirsute-stem plants but three failed to segregate any hirsute-stem plants. This segregation for hirsute-stem plants was consistent with the preceding evidence, that in certain genotypes heterozygous *Smsm* produced a hirsute-stem phenotype. The alternative explanation, that two independently inherited genes for glabrous stem had been present, was not supported by the frequency of hirsute-stem plants. More hirsute than expected had been observed in each segregating testcross. The modifying genes of the A subgenome appeared to affect *Sm* of *G. thurberi* more than the allelic *Sm* genes of *G. barbadense* and CS41235. However additional transferring of *Sm* of *G.*

Table 2. Segregation of stem hair in progenies having glabrous *G. thurberi* in their parentage.

Parentage	Population	Glabrous*	Hirsute*
F_1 ($2A_2D_1 \times 2A_2D_5$) $\times$ $2A_2D_1$	BC	1	1
1 hirsute BC plant $\times$ T2	TC	1	1
1 glabrous TC plant $\times$ T2	BC	5	7
1 hairy TC plant $\times$ T2	BC	0	16
F_1 ($2A_2D_1 \times$ St. Vincent) $\times$ T2	TC	5	4a
3 hirsute TC plants	TCF_2	17(2w)	26(1v)
1 glabrous TC plant	TCF_2	16	0
1 glabrous $\times$ T2	BC	5	2
F_1 ($2A_2D_1 \times$ St. Vincent) $\times$ CS 4125		12	0
glabrous No. 1 $\times$ T2	TC	6	6(1v)
2 $\times$ T2	TC	2	3
3 $\times$ T2	TC	5	4(3v)
4 $\times$ T2	TC	8	8(2v)
5 $\times$ T2	TC	7	6(6w)
6 $\times$ T2	TC	31	0
7 $\times$ T2	TC	10	0
8 $\times$ T2	TC	37(1w)	0

* (a) Appressed hair on stem. (w) Intergrade plants with single trichomes. (v) Portions of stem hairy, others glabrous.

thurberi to T2 and retesting against *Sm* of CS41235 has confirmed the dominance of both genes and their allelism. This procedure had eliminated the modifying genes of the A subgenome.

DISCUSSION

In this study of inheritance of glabrous stem a single, dominant gene was detected in each of five glabrous stocks. The *Sm* gene of T8Sm, which had been derived from diploid *G. armourianum* $2D_2$ according to Meyer (5), was allelic with the *Sm* gene of CS41235 and *G. barbadense* respectively. The distinction between *Sm* alleles of the two amphidiploid stocks probably is the duration of time each has been present in *hirsutum*. Coker Wilds also carries the CS41235 gene, and this quality cotton has been widely distributed.

Wild Socorro Island retained the long mane of hair on the upper side of some petioles that Fryxell and Moran (12) first noticed. Its glabrousness was demonstrated to result from a dominant *Sm* gene although other genes collectively produced an infrequent glabrous-stem phenotype in offspring of self-pollinated, hirsute plants. Saunders (8) encountered infrequent glabrous plants. Some of these genetically negated the expression of *H1*, a key gene for trichome initiation. He attributed this to the residual genotype. Analogously, the transferred *Sm* gene of Socorro Island, which seemed to be the key gene for glabrousness, segregated as if it were an allele of *Sm* of T8Sm. This conclusion was not overwhelmingly supported by the available information.

Only one *Sm* locus appeared to be involved when the trispecies F_1 ($2A_2D_1 \times$ St. Vincent) was outcrossed to CS41235 and then testcrossed to hirsute T2. *Sm* alleles of three sources must have been present in the outcross parents, but hair on stems was observed unexpectedly. The recovery of plants having hairy bolls and stems, resembling *H2H2* phenotype, suggested that hairy stem had been caused by interaction of *H* genes of the A subgenome and the *Sm* gene of the D subgenome. Both Ramey (7) and Saunders (10) reported that *H2* masked *Sm* and their interaction resulted in hairy-stem plants.

Independent evidence exists that *Sm* from *G. thurberi* and *Sm* of *G. armourianum* in T8Sm are genes of a common D subgenome chromosome. Phillips (6) showed that only one *Sm* gene of *G. armourianum* segregated in hexaploid hybrids. Kearney and Webber (3) studied F_2 of diploid *G. armourianum* $\times$ *G. thurberi* and reported no hair on plants and pictured none in cross sections of petioles.

The genetics of hair density is undoubtedly complex (12). Abundant hair under African environments meant the accumulation of A subgenome genes, H_1 initiator, *H3* stem-hair modifier, etc. Recently A subgenome *H2* appears to be replacing the *H1* system for hairy *G. barbadense* cultivars. Glabrousness meant the absence of *H1* and *H3* or H2 and sometimes certain genotypes (8, 9, 10).

Genetic explanations of hair density inheritance have areas of contradiction. For example, Empire cultivars of Smith (11) have a high hair density although *H1* is absent. Stem hair is removed by *h3*, an A subgenome gene (10), and by *Sm*, a D subgenome gene, when *H1* is present (7). Saunders (8) demonstrated that glabrous plants, which had no terminal hair as preceding phenotypes do, had *H1*. A study of Saunders' glabrous T.S.2 and *Sm* of Upland, both *G. hirsutum*, should be helpful in understanding the relationship of *h3* and *Sm*, as well as for obtaining glabrousness in *hirsutum* without using the *Sm* gene from *G. armourianum*. Smith (11) pointed to defects of *Sm* in Upland stocks and proposed that *Sm* not be used in the quest for decreased hair in American cultivars.

Finding *Sm* alleles in 2 *barbadense* and 2 *hirsutum* stocks and in 2 wild American diploid species suggests that *Sm* is not rare in *Gossypium* species of the New World. The presence of *Sm* raises the question of *sm* mutation to *Sm* in both amphidiploid and wild American diploids, especially if hairy *G. raimondii* (which has *sm*) is the most similar to the present D subgenome of the amphidiploids and since segregation frequencies in hexaploids (reported by Phillips (6)) exclude the introgression of *Sm* into the amphidiploids from glabrous *G. armourianum* and *G. thurberi*.

SUMMARY

Decreasing amounts of stem and leaf hair in Upland cotton was related with decreasing numbers of eggs placed on plants by moths of two *Heliothis* species. Therefore, a study of glabrous inheritance in five glabrous-stem sources was made. A single dominant gene, *Sm*, was found in each source. The *Sm* genes of *G. hirsutum* CS41235, *G. barbadense* Pima and St. Vincent, and transferred *Sm* of *G. armourianum* were allelic. During transfer from synthetic amphidiploid *G. arboreum-G. thurberi* to *G. hirsutum*, genes of the A subgenome interfered with glabrous-stem expression and reduced confidence that *Sm* of *G. thurberi* was allelic with *Sm* in *hirsutum*. The *Sm* gene of Socorro Island, a wild *G. hirsutum* relic, was sometimes tardy in removing stem hair but appeared to be allelic with *Sm*. Glabrousness in *G. hirsutum* may be manipulated by these D subgenome alleles of *Sm* and their combination with other genotypes which lack *H1* and *H2* of the A subgenome.

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