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Capitate Hairs on Cotton Leaves and Bracts[1]

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ABSTRACT

Significant differences in the capitate hair density of different cotton, *Gossypium hirsutum* L. and *G. arboreum* L., stocks were revealed by quantitative analysis of scanning electron micrographs of leaf and involucral bract epidermal surfaces. The density of capitate hairs on eight greenhouse-grown stocks ranged from 2.1 to 8.7 and from 4.7 to 31.6 per mm² on the adaxial and abaxial leaf surfaces, respectively. The capitate hair density on bracts of seven greenhouse-grown stocks ranged from 0.9 to 4.3 and from 3.4 to 8.6 per mm² on the adaxial and abaxial surfaces, respectively. There were significant differences among stocks in capitate hair density on both leaves and bracts. Capitate hairs were present on leaves of plants with the H_2, $Sm_1^{s1}Sm_2$, ne_1ne_2, or gl_2gl_3 mutant genes. There were no significant differences in capitate hair density on leaves of the same stock collected two years apart or on bracts collected from the same plant at anthesis or at 30 and 60 days postanthesis.

Additional index words: **Glandular hairs, *Gossypium arboreum, G. hirsutum,* Involucral bract, Trichomes.**

LEAF surfaces of higher plants include various epidermal outgrowth commonly referred to as hairs or trichomes. Two types of hairs occur on the foliage of cotton (*Gossypium* spp.): covering and capitate hairs (23). Covering hairs of higher plants are described as being morphologically simple, tufted, or stellate (4). In cotton, covering hairs are additionally characterized as erect or recumbent (21), by lengths of 0.25 to 2.0 mm (19), and by densities of zero to >300/mm² of epidermal surface (19). The density of covering hairs on the surface of cotton leaves is controlled by a number of mutant genes including H_1, H_2, Sm_1, Sm_2, and Sm_3 (9). Furthermore, covering hair density has been negatively correlated with populations of cotton leafperforator (*Bucculatrix thurberiella* Busck), leafhopper (*Empoasca* spp.) and spider mite (*Tetranychus telarius* L.) populations (14, 25) and positively correlated with fleahopper [*Psallus seriatus* (Reuter)] and *Heliothus* species populations 15, 16, 17).

Capitate hairs of higher plants are minute structures comprised of a stalk with a unicellular or multicellular head (5). In all *Gossypium* species examined by Webber (23) capitate hairs were observed on both the adaxial and abaxial leaf surfaces. These hairs on cotton contain phenolic substances (1) including isoquercetrin (2). In general, capitate hairs are thought to function in higher plants as specialized structures that elicit protective responses (14). For example, when the capitate hairs on epidermal surfaces of *Lycopersicon* and *Solanum* species are ruptured by the activities of aphids (*Aphis, Myzus,* or *Macrosiphum* spp.), they exude a sticky substance that hardens on the insect's limbs and thus immobilizes it (6, 8).

The study reported in this paper was undertaken to quantitate the density of capitate hairs on leaves and bracts of a number of commercial and primitive stocks of cotton including some that carry one of the following combinations of mutant genes: Pilose, H_2; glabrous, $Sm_1^{s1}Sm_2$; nectariless, ne_1ne_2; or glandless, gl_2gl_3.

MATERIALS AND METHODS

The following cottons (*Gossypium hirsutum* L. and *G. arboreum* L.) were used in this study: (A) Upland 'Paymaster 909,' 'Tamcot SP 21,' and 'Dunn 119;' (B) NR 145, *nectariless*, $ne_1ne_1ne_2ne_2$, from J. A. Lee, Raleigh, NC; (C) TM-1 (11) and H_2 *Pilose* (10) from R. J. Kohel, College Station, Tex; (D) Texas 1236 (T-1236), race *yucatanense,* from J. E. Quisenberry, Lubbock, Tex.; (E) VT glandless, $gl_2gl_2gl_3gl_3$, from J. E. Quisenberry, Lubbock, Tex.; (F) 542 glabrous, $Sm_1^{s1}Sm_1^{s1}Sm_2Sm_2$, from F. D. Wilson, Phoenix, Ariz.; (G) *G. arboreum,* SMA_4 glabrous, lintless from S. G. Stephens, Raleigh, N.C.

Paymaster 909, Tamcot SP 21, Dunn 119, NR 145, TM-1, H_2 Pilose, T-1236, and SMA_4 were grown in a greenhouse in 30 cm clay pots in a 1:1:1 clay, sand, and peat moss mixture. Leaf tissue was sampled when plants were 4 months old. Discs of leaf tissue, 6 mm in diameter, were removed on either side of the midrib at a point halfway between the basal and distal extremities of the lamina. To avoid possible effects of epidermal cell expansion and trichome abscission (6) on capitate hair density measurements, all cotton leaves sampled were the uppermost, fully-expanded leaves on the main axis. One leaf from three plants of each stock was examined in 1977 and again in 1979.

Discs of bract tissue, 6 mm in diam, were also obtained from three plants of greenhouse-grown stocks at anthesis, and again at 30 and 60 days postanthesis. Discs were removed from bracts at a point halfway between the involucral node and the distal extremity of the bract teeth.

The leaf and bract discs were fixed in 3.5% glutaraldehyde 0.1 *M* cacodylate buffer at pH 7.0 for 18 hours, dehydrated in an ascending series of ethanol and critically point dried in CO_2 (20). After having been coated with gold, the upper and lower surfaces were examined and photographed with the use of a Cambridge S4-10 scanning electron microscope. Twelve micrographs were taken of each sample. The density of capitate hairs and epidermal cells was determined from micrographs by $D = N/(A/M^2)$ where D is the density (no./mm²) and N is the number of hairs or cells counted in A area (mm²) of the micrograph at M magnification.

Leaf and bract samples were also collected in October 1979 from VT glandless and 542 glabrous stocks growing on Amarillo

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Table 1. Capitate hair density on mature leaves of cotton stocks.

Stock	Leaf surface*			
	Adaxial	Abaxial	Adaxial	Abaxial
	hairs/mm²		ratio†	
SMA_4	8.7 a	31.6 a	183 bc	66 d
T-1236	8.6 a	16.4 b	139 c	103 cd
TM-1	5.0 b	7.4 c	150 bc	128 bc
NR 145	4.5 bc	8.3 c	209 b	132 bc
Dunn 119	3.8 bcd	7.4 c	171 bc	121 c
H_2 Pilose	3.7 cd	7.0 c	272 a	171 ab
Paymaster 909	2.8 de	4.7 d	192 bc	147 bc
Tamcot SP 21	2.1 e	4.9 d	305 a	206 a

* Means within a column followed by the same letter were not different at the 0.05 probability level, according to Duncan's Multiple Range Test.
† Ratio = number of tabular epidermal cells divided by the number of capitate hairs.

loam (Aridic Paleustalfs) in a field in Lubbock County, Tex. Sampling procedures and processing of tissue discs were the same as described for greenhouse stocks.

RESULTS AND DISCUSSION

A typical surface of a cotton leaf with capitate hairs, numerous epidermal cells, and many stomata is shown in Fig. 1. The capitate hairs on leaf and bract epidermal surfaces of cotton are multicellular (10 to 12 cells) structures consisting of 1 or 2 foot cells, one stalk cell, and two or three tiers of head cells (22). These hairs are approximately 40 μm in diam and 50 μm tall; they occur most frequently over minor veins (Fig. 2). Capitate hairs as a group are morphologically distinct from the larger glandular hairs or multicellular papillae (24) of the extrafloral nectaries of cotton.

The density of capitate hairs on leaves ranged from 2.1 to 8.7 and from 4.7 to 31.6/mm² for the adaxial and abaxial surfaces, respectively for eight greenhouse-grown stocks (Table 1). Because numerous factors, including salt-stress, can affect leaf area (3, 18), the populations of these hairs on the same greenhouse stocks were also quantitated as the ratio of the number of tabular epidermal cells to capitate hairs (Table 1). The epidermal cell-capitate hair ratio was found to vary from 139 to 305 and from 66 to 206 for the adaxial and abaxial surfaces, respectively. Both methods of estimating capitate hair population show that more of these hairs were found on the abaxial than on the adaxial leaf surface.

The density of capitate hairs on leaves of greenhouse stocks was significantly ($P < 0.01$) correlated for collections made 2 years apart ($r = 0.98$ and 0.99 for the adaxial and abaxial surfaces, respectively from the 1977 and 1979 leaf samples of the eight stocks). Thus, there was little effect of environment on capitate hair density within stocks from year to year. Highly significant correlation coefficients ($P < 0.01$) were also obtained between adaxial capitate hair density and each of the following leaf epidermal parameters: abaxial capitate hair density ($r = 0.87$), adaxial epidermal cell density ($r = 0.88$), and abaxial epi-

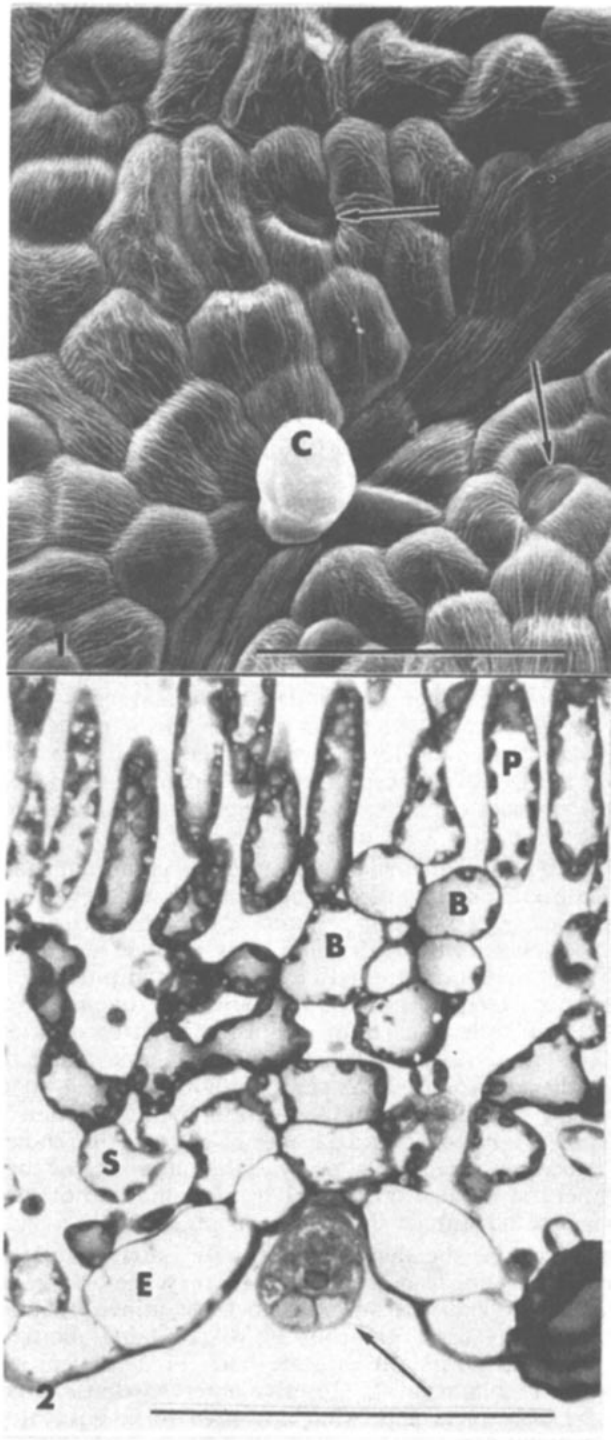

Fig. 1 to 2. ***Fig. 1.*** **Scanning electron micrograph of a cotton leaf showing a capitate hair (C), numerous epidermal cells, and several stomata (arrows). This capitate hair is located over a minor vein. Scale line = 100 μm. × 410.** ***Fig. 2.*** **Light micrograph of a longitudinal section of a multicellular capitate hair (arrow) on the abaxial surface of a cotton leaf. Also shown are epidermal cells (E), spongy mesophyll cells (S), palisade cells (P), and several bundle sheath cells (B) around a minor vein. Scale line = 100 μm. × 530.**

Table 2. Capitate hair density on involucral bracts (flowers at anthesis) of cotton stocks.

Stock	Bract surface*	
	Adaxial	Abaxial
	hairs/mm²	
H_1 Pilose	4.3 a	7.7 a
SMA_4	3.5 b	4.1 b
TM-1	2.4 c	8.6 a
Tamcot SP 21	1.8 d	7.6 a
Paymaster 909	1.6 de	7.7 a
Dunn 119	1.0 ef	3.4 b
NR 145	0.9 f	7.8 a

* Means within a column followed by the same letter were not different at the 0.05 probability level, according to Duncan's Multiple Range Test.

dermal cell density (r = 0.90). Significant correlation coefficients ($P < 0.01$) were also recorded between abaxial capitate hair density and the following epidermal parameters: adaxial epidermal cell density (r = 0.93), abaxial epidermal cell density (r = 0.94), and the density of stomata (no./mm²) on the abaxial surface (r = 0.87).

Regardless of whether capitate hair populations were quantitated with reference to leaf surface area or to the number of tabular epidermal cells, there were significant differences among stocks in the density of these hairs for a given epidermal surface (Table 1). Density of capitate hairs was highest on both leaf surfaces of SMA_4 and among the lowest on both leaf surfaces of Tamcot SP 21.

Different densities of capitate or glandular hairs also occur on the adaxial and abaxial surfaces of mature leaves of *Solanum* (6) and *Medicago* species (13). Experiments with different plants of these species indicate that capitate hairs can be manipulated by breeding techniques (7, 13). Assuming that the average mature leaf of cotton has a surface area of about 10,000 mm² (21), it is estimated from Table 1 that the number of capitate hairs per leaf (both surfaces) varied from 7×10^4 to 4×10^5. Although the function of capitate hairs on mature leaves of cotton is unknown, the occurrence of large, but variable, numbers of these structures on leaf epidermal surfaces may be of some selective advantage to the cotton plant.

In cotton, the density of capitate hairs on mature leaves was not associated with the presence or absence of covering hairs because the stocks examined included Pilose (H_2) and glabrous (SMA_4) plants, both of which had abundant capitate hairs on both leaf surfaces. Lukefahr et al. (16) also observed that capitate hairs were present in what appeared to be equivalent numbers on young leaves of both Pilose and glabrous strains. NR 145, a nectariless stock, had as many capitate hairs as the nectaried stocks, showing that ne_1 and ne_2 (which remove most of the glandular hairs of the extrafloral nectaries) did not remove the capitate hairs from the surfaces of the same leaves.

Because of the difficulty of seeing the anticlinal walls of tabular epidermal cells on leaves of the field-grown plants of 542 glabrous and VT glandless, capitate hairs could be quantitated only in terms of their numbers. The glabrous stock had 14.5±0.4 ($\bar{x} \pm s_{\bar{x}}$, $N=3$) and 15.8±1.0 capitate hairs/mm² on the adaxial and abaxial leaf surfaces, respectively. Capitate hair density on the adaxial and abaxial leaf surfaces of the glandless stock was 8.6±0.2 and 8.6±0.5/mm², respectively. Although these observations have not been repeated on a second field-grown crop, the two stocks sampled in the single test had a consistent population of capitate hairs on their leaves. Glabrousness conferred by Sm_1^{sl} and Sm_2, and the glandlessness caused by gl_2 and gl_3, did not remove capitate hairs from cotton leaf surfaces.

The density of capitate hairs on bracts of seven greenhouse stock ranged from 0.9 to 4.3 and from 3.4 to 8.6/mm² on the adaxial and abaxial surfaces, respectively (Table 2). As with leaves, significant differences in density were found among stocks for both bract epidermal surfaces. Comparison of Tables 1 and 2 shows that densities of capitate hairs on leaf and bract surfaces are not necessarily correlated. For example, the density of capitate hairs on the abaxial bract surface of SMA_4 is lower than that on the bracts of most other stocks (Table 2). By contrast, the density of hairs on the abaxial leaf surface of SMA_4 is higher than that on any other stock (Table 1). Differences in capitate hair density found on various plant parts have also been reported for *Solanum* species (6).

Bracts collected from field-grown 542 glabrous plants had capitate hair densities of 2.4±0.8 and 12.9±1.0/mm² for the adaxial and abaxial surfaces, respectively; comparable values for VT glandless were 0.0 and 3.7±0.7/mm². The adaxial surface of VT glandless bract was the only cotton plant part surface observed that was devoid of capitate hairs.

The density of capitate hairs on the abaxial bract surface of greenhouse-grown Paymaster 909 was 8.5±0.7/mm² at anthesis, 7.6±0.3/mm² at 30 days postanthesis, and 8.1±0.8/mm² at 60 days postanthesis. Differences among collection dates were not significant indicating that capitate hair density was established prior to anthesis. Capitate hairs on the abaxial cotton bract surface, unlike similar trichomes on the basal leaves of *Solanum* species (6), did not abscise. The density of capitate hairs on cotton bract surfaces was constant on whole bracts collected from greenhouse and field-grown stocks as well as on the surfaces of bract fragments entrained in ginned cotton lint (12). Thus, capitate hairs might have a role in such diverse phenomena as byssinosis etiology (12) and in the inhibition or stimulation of insect populations. Only future research on these structures will confirm or refute these speculations.

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