Some Problems in Breeding Smooth-Leaved Cottons¹

Joshua A. Lee²

ABSTRACT

Four alleles distributed at three independent loci impart varying degrees of smoothness to the leaves of upland cotton, Gossypium hirsutum L. Each of these alleles, when homozygous, and acting free of other smoothness alleles, confers a characteristic degree of smoothness. Certain interallelic combinations increase smoothness, whereas others do not. Some problems in breeding for smoothness are: (a) determining the degree of smoothness needed, (b) selecting the alleles necessary to impart that level of smoothness, and (c) recognizing the effects of the smoothness alleles in the background chosen, particularly in the heterozygous state. There is little reason to believe that individual smoothness alleles impart any undesirable traits other than possible susceptibility to thrips. However, certain allelic combinations might lower lint percent, and certain of the alleles could be linked to genes conditioning agronomically undesirable traits.

Additional index words: Trichome, Pubescence, Gossypium hirsutum L., Gossypium barbadense L.

S MOOTH-LEAF describes a condition in upland cotton, Gossypium hirsutum L., where there are decidedly fewer trichomes on the leaves than are usually encountered. Cottons with smooth leaves produce cleaner grades of ginned lint than pubescent varieties (3). Moreover, plant smoothness is of potential value in providing host resistance to certain insect pests (11, 12). Thus smoothness could increase agronomic adaptation of cotton in many regions where the crop is grown.

The problems confronting the breeder who seeks to make adapted varieties more glabrous are at least three in number: (a) the degree of smoothness needed must be ascertained, (b) the alleles needed to impart the degree of smoothness desired have to be selected and, (c) the alleles must then be transferred into the stocks that have been selected for improvement.

Discussion of the first problem is, in general, beyond the scope of this report. However, information about the expressivity of individual alleles, and various combinations thereof, could help breeders in making them aware of the possibilities and limitations inherent in the currently available resources. Answers to the second problem can be had through reference to genetic studies concerning the smooth-leaf character, several of which will be reviewed herein. The

third is likewise within the scope of this report, and some of the problems likely to be encountered in this particular area will be discussed in detail. Most of the current report is based upon a review of the pertinent literature. The remainder stems from work performed recently at the North Carolina Agricultural Experiment Station by the author.

GENETIC RESOURCES

The genetic resources for the smooth-leaf character have been described previously (10). Currently there are available four alleles distributed at three loci, each capable, at least when homozygous, of bestowing a characteristic level of smoothness to the plant's leaves. Some of the alleles remove trichomes from stems as well. The phenotypic expressions of the various alleles will be described briefly.

The sm_1 locus. There are three alleles at the sm_1 locus. The recessive allele, sm1, determines normally pubescent plant when acting in concert with alleles of similar expression at other loci. A second allele, Sm_1 , removes trichomes from stems, exerting only minor effects on leaves (9). The third allele, Sm_1^{s1} , when homozygous and acting free of other smooth-leaf alleles, imparts a high level of leaf smoothness, and simultaneously removes most of the trichomes from the stems. Mature leaves of plants homozygous for Sm₁⁸¹ have trichomes distributed about the leaf margins with a small number persisting on the principal veins in the regions adjacent to the pulvinus. Juvenile leaves are more pubescent than mature leaves; these often have a dense crop of pubescence on the leaf margins and principal veins. Most of the trichomes on veins are sloughed off as the leaf matures; the only ones which have a strong tendency to persist are those about the leaf margins. This shedding of trichomes occurs in both the greenhouse and the field, so it is not altogether a matter of the trichomes weathering away, although wind and rain could conceivably aid the process. Sources of Sm_1^{81} are available in those cottons descending from Meyer's 'D₂ Smooth' (13). Other sources are available in 'Coker 413', a commercial variety released by the Coker's Pedigreed Seed Company3, in 'Kerr's Smooth', and in 'Line B Smooth'. These latter two strains were selected by D. C. Harrell at the U. S. Field Station, Florence, South Carolina. It is commonly believed that sources of $Sm_1^{s_1}$ in upland cotton other than \mathbf{D}_2 smoothness originate from introgression with Gossypium barbadense L. However, this is conjecture and has not been established as fact.

The sm_2 locus. Other than the normal allele, sm_2 , there is one smooth-leaf allele at this locus. Sm_2 when homozygous, and acting free of other smooth-leaf alleles, imparts a degree of smoothness similar to that bestowed by $Sm_1^{s_1}$. The total expressions of the two alleles are similar in that both allow an appreciable number of trichomes to develop on juvenile leaves, trichomes that are largely lost as the leaf matures. In most upland backgrounds that I have used, Sm_2 gives slightly smoother mature leaves than $Sm_1^{s_1}$, and the margins of the bracteoles are usually devoid of trichomes.

 Sm_2 was introduced into upland cotton from the commensal, or house-yard cotton, Wh-219, by Lee (10). It is now available in the varietal backgrounds, 'Carolina Queen,' 'Auburn 56', and 'TH-149'. The first two cottons were released under the designations, 'North Carolina Smooth,' lines 1 and 2. The LAMSL lines, produced at the Texas Experiment Station by G. A. Niles are homozygous for Sm_2 , as determined by tests performed at the North Carolina Experiment Station. However, the possibility that LAMSL lines harbored other smooth-leaf alletes was not ruled out. According to Niles (14) and Jones (6) these lines trace their smoothness to commensal cottons from Yucatan.

¹ Contribution from the Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, and the Department of Crop Science, North Carolina Agricultural Experiment Station, Raleigh, N. C. 27607. Paper No. 335I of the Jorunal Series. Received December 9, 1970.

² Geneticist, Crops Research Division, ARS, USDA.

³ Mention of cotton varieties and firms that breed and merchandise them is meant for illustrative purposes only, and does not imply endorsement by the USDA of the varieties, or the activities of the firms.

4350653, 1971, 3, Downloaded from https://access.onlinelibrary.wiley.com/doi/10.2155/cropsci1971.0011183X001100030043x by North Carolina State Universit, Wiley Online Library on [19/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley

.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons

The sm_3 locus. There are three alleles at the sm_3 locus, and two of these impart at least partial smoothness to the leaves. The Delta Smoothleaf allele (5), sm_3 , restricts trichomes to the principal leaf veins, the leaf margins, and the stems. Thus its expression is similar to that noted in juvenile foliage of plants homozygous for $Sm_1^{s_1}$ or Sm_2 , the chief difference being that the trichomes are retained in plants homozygous for sm_3 . This allele is recessive to the normal allele at this locus, sm_3^{h} . The third allele, Sm_3 , is dominant to normally pubescent, and, in either the homozygous or heterozygous state, gives a phenotype similar to that of sm_3 when it is in the homozygous state. Sm_3 was found in WH-219 in company with Sm_2 (10). Stocks bearing Sm_3 have not been released for breeding purposes.

The recessive allele, sm_3 , is widespread in adapted varieties of upland cotton; and is, to date, the most widely used of the smooth-leaf alleles in breeding programs. At least two varieties offered by the Delta and Pine Land Company are homozygous for this allele, as is 'Rex Smooth-leaf,' a variety developed at the Arkansas Experiment Station. A phenotypic identical to that imparted by sm_3 has been noted in 'Acala 4-42.'

ALLELIC COMBINATION

Some gains in smoothness can be obtained from combining certain of the smooth-leaf alleles in the homozygous state. The most noticeable gains are on the juvenile leaves. Lukefahr et al (12) have shown that the glabrous terminals of such plants provide resistance to the fleahopper (*Psallus seriatus* Reuter) in South Texas.

Combinations involving Sm_2 with either $Sm_1^{\rm sl}$ or Sm_3 provide "ultra-smoothness." The leaves of plants of these genotypes are devoid of trichomes when mature (10). In upland backgrounds juvenile leaves may have a few trichomes about their margins, but these are lost as the leaf matures.

I have synthesized stocks of the genotype $Sm_1^{sl}Sm_1^{sl}$ $Sm_2Sm_2Sm_3Sm_3$, and these are also ultra-smooth. Plants bearing the trimeric combination lack even the few trichomes noted on the terminal of the dimeric types described above. However, the gain in smoothness is seemingly too small to warrant synthesizing this genotype in a breeding program. The plants containing dimeric combinations involving sm_3 that I have produced have not given ultra-smoothness but may be slightly smoother than plants homozygous Sm_1^{sl} or Sm_2 .

SOME BREEDING PROBLEMS

One important problem that confronts breeders in their attempts to use smooth-leaf concerns recognition of the character at successive stages in a breeding program, and in the particular background into which it is being introduced. Any of the smooth-leaf alleles should be clearly recognizable in the homozygous state in virtually all backgrounds known in commercial cottons. In fact Ramey (15) has shown that D₂ smoothness (Sm1sl) is epistatic to the hairiness alleles in 'Mu-8b. This very pubescent cotton is homozygous for H_1 , an allele that causes pubescence to be more dense and greater in length than is usually the case with upland cottons (8, 16). It is unlikely that breeders will encounter many cottons that are more pubescent than Mu-8b, so any of the smoothness alleles should confer a recognizable degree of smoothness on any background found in modern commercial uplands. Ramey (15) also shows that the Pilose allele, H_2 , is, on the other hand, epistatic to D₂ smoothness. Working smoothness into such an exceptionally hirsute background could pose special problems. To my knowledge, no commercial upland cotton harbors H_2 .

Being able to recognize the presence of a smoothness allele in the heterozygous state should facilitate breeding progress. In my experience, the effects of all of the smooth-leaf alleles, with the exception of sm_3 , are recognizable in the heterozygous state. In fact Sm_3 proved to be dominant in all of the backgrounds tried. However, it has not been introduced into backgrounds containing H_1 . Thus if Sm_3 should become available for use in breeding programs, it should be readily recognizable in single dose in many different backgrounds. Although Meyer (13) stated that the D_2 form of Sm_1 ^{sl} is dominant to its normally pubescent allele, sm_1 , I have found that both it and Sm_2 vary somewhat in expression in the heterozygous state, depending upon the background. If the cotton is only moderately pubescent, such as is the case with 'Carolina Queen,' and 'Deltapine 15,' both $Sm_1^{\rm sl}$ or Sm^2 appear to be dominant. In more pubescent backgrounds, such as 'Empire', the expression is intermediate, and in some backgrounds, such as Mu-8b, the F₁ is noticeably pubescent. However, in all backgrounds that I have examined both Sm_1^{sl} and Sm_2 impart a smoother phenotype in the F_1 than that of the more pubescent parent. Thus with Sm_1^{sl} and Sm_2 only approximate predictions can be made about the phenotypes of F₁ plants in subsequent generations in a breeding program. The breeder should acquaint himself with the expression of these alleles in the particular background to be used, and let the experience gained be his guideline. If he can recognize the heterozygotes in each generation the savings in time and resources should amply reward his efforts. With sm_3 recognition of heterozygotes does not seem possible, so the breeder must resort to homozygous to be assured of the presence of this allele.

Most of the American upland cottons that I have observed have more trichomes on the lower leaf surface than on the upper surface. Thus a diminution in trichome count on the lower surface is more likely to indicate the presence of a smooth-leaf allele than the phenotype of the upper surface. Therefore one might gain by basing selections on the phenotype of the lower leaf surface.

What are the chances that the various smooth-leaf alleles will impart undesirable pleiotropic effects, or will be linked with germplasm that conditions undesirable traits? Since the lint hairs on seeds are modified trichomes one might reasonably expect that drastic reduction of leaf trichomes would interfere with the production of lint hairs. Davis (1) found that the D_2 Smooth morph of $Sm_1^{\rm sl}$ lowered gin out-turn about 2% in New Mexico when in an 'Acala 1517' background. Using the same allele Jones (7) experienced about 1% reduction in gin out-turn for the 'Bayou' variety in Louisiana. Niles (14) found severe reductions in lint percentage (gin out-turn) with the LAMSL lines discussed earlier. This loss could have been caused by the presence of Sm_2 . At the North Carolina Station I have but one small test comparing the performance of lines bearing Sm_2 and their recurrent parental varieties. This test was performed at the Upper Coastal Plains Experiment Station, Rocky Mount, North Carolina, in 1970. There were four replications per entry. The "TH-149" smooth accession yielded about 1% more in gin out-turn than its normal recurrent parent, and the 'Carolina Queen'

4350653, 1971, 3. Downloaded from https://acsess.onlinelibrary.wiley.com/doi/10/2135/cropsci1971.0011183X00110030043x by North Carolina State Universit, Wiley Online Library on [19/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley on Wiley Online Library for rules of use; OA articles are governed by the

smooth equivalent line about 1% less than its check. Thus what evidence there is suggests that in North Carolina, at least Sm_2 might not exact a penalty in gin out-turn; or, at most, no more than D₂ Smooth at some other sites.

However, combinations involving two or more of the more potent smooth-leaf alleles could result in problems. I have preliminary evidence that such combinations can drastically reduce lint percent. Before a definitive statement can be made concerning the undesirability of combining smooth-leaf alleles more research is needed.

Smith (17) expressed the opinion that the D_2 Smooth morph of Sm_1^{sl} was related to undesirable traits, particularly a tendency to make the variety bearing it later and less productive than similar, pubescent varieties. Neither Davis (1) nor Jones (7) found that D2 Smooth significantly reduced fiber yield in their material. However, Jones found that smooth lines were somewhat later than their pubescent sibling lines. Thus is appears that if D₂ Smooth is associated with deleterious agronomic traits they can be at least partially ameliorated through breeding, possibly through changes in linkage relationships. Another form of Sm_1 ^{sl} has been used in the commercial variety 'Coker 413,' apparently with success. This gene does not derive from D_2 Smooth material (18).

In the varieties 'Carolina Queen' and 'Auburn 56' Sm_2 does not appear to alter earliness and productivity at the Central Crops Research Station, Clayton, North Carolina, where the smooth lines were bred. About 80 km (50 miles) away smooth-leaf 'Carolina Queen' was late and unproductive, as was the smooth-leaf equivalent of 'TH-149' (Table 1). Apparently Sm_2 is linked with germplasm that can produce striking environmental interactions for rate of maturity; which, in turn, causes reduction in lint yield. To my knowledge, stocks bearing Sm_3 have been grown only at the Central Crops Research Station. There they appear to be early and productive.

The Delta Smooth allele (sm_3) has been used in commercial upland cottons for at least 20 years (2) with no documented losses in performance attributable to the presence of Smooth-leaf. Cottons bearing sm₃ have been utilized throughout the American cottonbelt as well as in cotton growing regions abroad. There fore there is little evidence that this allele, or the germplasm associated with it, carries agronomically undesirable traits.

Other than possibility that smooth-leaf might condition greater susceptibility to thrips in some regions (4) it does not appear that smooth-leaf is per se agronomically deteterious. This claim takes weight from the widespread use of sm₃, and at least one source of Sm₁sl. There is evidence that some other smooth-leaf

alleles are linked with undesirable germ plasm, and the breeder should approach the problem of combining alleles at different loci with caution. Linkage associations can be changed. Testing of the products of breeding in multiple environments is recommended.

LEAF SMOOTHNESS IN Gossypium barbadense

Commercial varieties of G. barbadense are generally regarded as being glabrescent (8); that is to say, juve-

Table 1. Relative fiber yields of normally pubescent cotton varieties and their smooth-leaved off-spring.

Entry	Lint %	Fiber yield in grams per 15, 25-meter plot
rolina Queen	41, 2	1,850
Carolina Queen Smooth	39.9	1,303
TH-149	36.8	2,004
TH-149 Smooth	37.8	1,695

nile foliage is somewhat pubescent, the trichomes being lost as the foliage matures. Personal observations suggests that this is not the case, since what trichomes there are initially seem to persist. Nevertheless, many cultivated G. barbadense cottons have very few trichomes on the leaves, and the stems of most of these are glabrous. Among familiar forms Sea Island is perhaps the least pubescent of G. barbadense cottons, whereas the newer Pima varieties 'Pima S-3', and 'Pima S-4', are virtually as hairy as some of the "low-

grade," normally pubescent, upland cottons.

If one crosses 'Seabrook Sea Island' cotton with a broad spectrum of upland varieties he can obtain plants that are entirely glabrous in the F2 of virtually all crosses. Recently I used such a segregate to establish a glabrous line of 'Coastland', a modern Sea Island strain bred by Julian Jenkins at the Coastal Plains Station, Tifton, Georgia. The genetics of this smoothness has not been determined, but observations on segregating populations suggest that it is simply inherited in 'Sea Island' background. Should leaf smoothness ever be needed in G. barbadense this newly synthesized source could be of use.

REFERENCES

- Davis, Dick. 1969. Agronomic properties of smooth, nectari-less 'Acala' cotton. Crop Sci. 9:817-819.
- 2. Ewing, Early C., Jr. Personal communication. 3. ———, E. L. Gilbert, and W. W. Bradford. 1958. The cleaning of smooth leaved cottons. Proc. Eleventh Ann. Cot. Imp.
- 4. Hawkins, B. S., H. A. Peacock, and T. E. Steele. 1966. Thrips injury to Upland cotton (Gossypium hirusutm L.) varieties. Crop Sci. 6:256-258.
- 5. Isaac, S. A., Jr., and M. T. Henderson. 1951. Inheritance of leaf pubescence in Upland cotton. Agron. J. 43:99.
- 6. Jones, J. E. Personal communication.
- , L. W. Sloane, and A. J. Major. 1971. Isogenic studies of D₂ smoothness in upland cotton. Proc. Twenty-third Ann.
- Cot. Imp. Conf. (Abstract).
 Knight, R. L. 1952. The genetics of jassid resistance in cotton. I. The genes H₁ and H₂. J. Genet. 51:46-56.
 Lee, Joshua A. 1966. Genetics of the smooth-stem character in Computing Leaving L. Con Sci. 6:407-408.
- in Gossypium hirsutum L. Crop Sci. 6:497-498.
- 1968. Genetical studies concerning the distribution of trichomes on the leaves of Gossypium hirsutum L. Genetics 60:567-575.
- Lukefahr, M. J., C. B. Cowan, T. R. Pfrimmer, and I. W. Noble. 1966. Resistance of experimental cotton strain 1514 to the bollworm and cotton fleahopper. J. Econ. Entomol. 59:393-395.
- Cotton strains resistant to the cotton fleahopper. J. Econ. Entomol. 61:661-664.
- Meyer, J. R. 1957. Origin and inheritance of D₂ smoothness in Upland cotton. J. Hered. 48:249-250.
- 14. Niles, G. A. Personal communication.
- 15. Ramey, H. H. 1962. Genetics of plant pubescence in Upland cotton. Crop Sci. 2:269.
- 16. Saunders, J. H. 1961. The mechanism of hairiness in Gossypium. Heredity 16:331-348.
- Smith, A. L. 1964. Leaf trichomes of Upland cotton varieties. Crop Sci. 4:348-349.
- 18. Webb, Henry. Personal communication.