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Allele Determining Rugate Fruit Surface in Cotton[1]

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ABSTRACT

Rugate fruit surface in cotton (*Gossypium hirsutum* L.) is accompanied by dense glandulosity and correlates with increased terpenoid aldehyde level in flower buds. Rugate carpellary surface is determined in M. J. Lukefahr's XG-15 line by the allele Gl^r_3 in the homozygous state acting in concert with an array of other gland-determining alleles at other loci. A sister line, 3-T, is homozygous for Gl_3, an allele having little or no capacity to impart rugate fruit surface. Gl^r_3 was transferred to two stocks of *G. barbadense* L. where the allele also produced densely glanded, rugate fruit surface.

Additional index words: **Cotton, Terpenoid aldehyde, Gossypol, *Gossypium barbadense* L.**

THE fruit surfaces of American cultivars of Upland cotton (*Gossypium hirustum* L.) are nearly or entirely smooth, as are those of the majority of the wild and ruderal forms of the species that I have observed. A few stocks of *G. hirsutum* have a rugate, or pitted, boll surface. Some of these cottons are West Indian accessions of the race (*marie-galante*) (6), whereas others can be traced to cottons selected by M. J. Lukefahr (5) for high terpenoid aldehyde (1) content in fruiting forms or squares.

Lukefahr's experimental line, XG-15, seems typical of these high terpenoid cottons. The surface of the ovary of this stock is virtually blackened with pigment glands as the flowers approach anthesis. Low terpenoid stocks, such as Upland cultivars, may display a large number of glands on mature bolls, but these glands are not well developed at anthesis. In XG-15 the expansion of the ovary after pollination is accompanied by an increasingly rugate carpellary surface, apparently as a result of differential growth of itssues between glands and those immediately surrounding the glands. Thus at maturity most of the glands lie in shallow depressions on the surface of the fruit.

Lee (3) implicated the Gl_3 (secondary leaf gland) allele as the carrier of primary potency for the expression of rugate fruit in XG-15. This hypothesis was based on the fact that when the leaf gland alleles, Gl_2 and Gl_3, were separated into monomeric stocks, fruits of plants homozygous for Gl_3 were rugate whereas those homozygous for Gl_2 were not. Moreover, fruit surfaces of Gl_3 were more glandular than those of plants homozygous for Gl_2. Recently Wilson and Smith (7) have shown heightened terpenoid activity centering around the Gl_3 allele in their stocks.

These results, though suggestive, do not exclude the possibility that alleles other than Gl_3 carry primary potency for the rugate phenotype with Gl_3 functioning in a supportive role. The following experiments were designed to determine if an allele at gl_3 locus carries primary potency for rugate fruit surface in XG-15 and to evaluate the possibility that other alleles play a supportive role.

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Table 1. Phenotypes associated with various genotypes in XG-15 and 3-T†.

Stock		Genotypes			
		$2(Gl_2Gl_3)$	$2(Gl_2gl_3)$	$2(gl_2Gl_3)$	$2(gl_2gl_3)$
XG-15	Gland density‡	(64.6 ± 1.5)	(63.2 ± 2.6)	(97.2 ± 2.0)	0
	Fruit texture	Rugate	Nearly smooth	Rugate	Smooth
3-T	Gland density	(51.4 ± 1.9)	(26.6 ± 1.8)	(19.6 ± 2.1)	0
	Fruit texture	Nearly smooth	Smooth	Smooth	Smooth

† Ten greenhouse-grown bolls sampled for each genotypic entry. ‡ Mean gland number per cm² of boll surface with standard error.

MATERIALS AND METHODS

The experimental materials consisted of various genotypic stocks of the *G. hirsutum* lines, XG-15 and 3-T, as follows: dimeric, $Gl_2Gl_2Gl_3Gl_3$; monomeric, $Gl_2Gl_2gl_3gl_3$ and $gl_2gl_2Gl_3Gl_3$; and nullomeric (glandless), $gl_2gl_2gl_3gl_3$. These stocks were remnants from earlier experiments on gossypol levels in cottonseed (4); and in addition to differing widely in seed gossypol level, they display broad variation in leaf and fruit glandulosity. The following *G. barbadense* L. stocks were used: glandless forms of both AS-2 Sea Island and 'Pima S-4', and monomeric ($Gl_2Gl_2gl_3gl_3$ and $gl_2gl_2Gl_3Gl_3$) AS-2 Sea Island.

Six experiments were conducted as follows: (i) gland counts and visual estimates of fruit rugosity were made on the dimeric, monomeric, and glandless entries of XG-15 and 3-T to demonstrate the phenotypic differences that exist among the various glandulosity genotypes of these cottons; (ii) XG-15 plants, monomeric for Gl_3, were crossed with glandless XG-15 and an F_2 population scored to demonstrate in a formal way the relationship between Gl_3 in the homozygous state in this cotton and the presence of densely glanded, rugate fruit; (iii) XG-15 plants, monomeric for Gl_3, were crossed with glandless 3-T and F_1 and F_2 populations were scored to determine if the 3-T background was comparable to that of XG-15 in terms of potential for sustaining the expression of densely glanded, rugate fruit; (iv) 3-T plants, monomeric for Gl_3, were crossed with glandless XG-15, and F_1 and F_2 populations were scored to determine if the Gl_3 allele from 3-T could substitute for that of XG-15 in imparting densely glanded, rugate fruit surface; (v) Gl_3 alleles from both XG-15 and 3-T were transferred to glandless *G. barbadense* to determine if the allele from either source was capable of imparting rugate fruit surface in the new background; (vi) the Gl_2 and Gl_3 alleles of the *G. barbadense* stock, AS-2 Sea Island, were transferred to both glandless XG-15 and glandless 3-T to determine if the *G. barbadense* alleles imparted rugate fruit surface in the *G. hirsutum* backgrounds.

All crosses were made in a greenhouse, and all population for scoring were grown in a field during the years 1973 through 1975. Conditions of temperature and rainfall were variable from year to year, but they influenced gland phenotype very little. Field-grown plants received two to three supplemental irrigations during July of each year.

RESULTS AND DISCUSSION

Experiment 1. All glanded entries of XG-15 displayed significantly more glands per cm² of mature boll surface than their genotypic counterparts in 3-T (Table 1). Fruits of dimeric and Gl_3 monomeric plants of XG-15 were the most rugate (Fig. 1). The Gl_3 monomeric in XG-15 averaged more glands per cm² squared of boll surface than any other entry. These glands appeared to be smaller than those produced by the dimeric stock of either XG-15 or 3-T, or the Gl_2 monomeric in XG-15. In XG-15 the Gl_2 allele seems to determine gland number on bolls, and perhaps to a large extent, size; whereas Gl_3 seems to determine early penetrance of glands on the ovary, which, as mentioned before, relates to rugate fruit surface on mature bolls.

Although the 3-T dimeric produced more than 50 glands per cm² of boll surface, the fruits were only faintly rugate. Neither of the 3-T monomerics approached their genotypic counterparts in XG-15 in gland number, and the fruit surfaces of both were smooth.

Dimeric XG-15 and 3-T differ in their seed terpenoid (gossypol) potentials. While the former commonly assays 2.00 to 2.10% in seed gossypol, the latter averaged 2.78% in two trials (4). However, the higher potential for terpenoid production in 3-T does not penetrate into flower buds. Assays of flower bud material at Raleigh, N.C. have shown that dimeric XG-15 ranges from 1.50 to 1.75% terpenoid aldehydes in freeze-dried flower bud powder, whereas no samples of dimeric 3-T grown in a comparable environment (greenhouse) exceeded 0.90%. Flower buds of the Gl_3 monomeric in XG-15 averaged about 1.20% whereas neither monomeric in 3-T ranged higher than 0.30%.

Experiment 2. Fruit surfaces of F_1 plants following the cross of glandless and Gl_3 monomeric stocks of XG-15 were densely stippled with minute glands but not rugate. The F_2 consisted of 25 plants with glandless bolls; 56 displayed the F_1 phenotype, and 30 had glanded rugate bolls. These data fit the expected 1:2:1 ratio very well ($P=0.75$ to 0.9). A consistent relationship between Gl_3 in the homozygous state in XG-15 and the occurrence of rugate fruit surface was thus confirmed.

Experiment 3. Because XG-15 and 3-T are sibling lines and both have high potentials for terpenoid expression, I speculated that the two differed principally in that the former had a special, high glandulosity allele at the gl_3 locus. If that were the case, an F_2 stemming from the cross of the Gl_3 monomeric in XG-15 and glandless 3-T should produce the same array and proportions of phenotypes recovered in Experiment 1.

The actual recovery from the cross was quite different from that in Experiment 1. Bolls of F_1 plants varied from glandless to sparsely glandular, there being variation among the fruits on individual plants. Fruit surfaces of the 142 F_2 plants ranged from glandless to densely glanded and smooth, to densely glanded and rugate. The phenotypic array did not fit a simple segregation ratio as in Experiment 1.

Selfing of selected progenies produced both smooth and rugate-fruited monomerics. These results were interpreted to mean that the Gl_3 allele in XG-15 is only conditionally potent for the production of the rugate phenotype. Apparently, "supportive" alleles are needed to interact with Gl_3 to produce the phenotype. Those alleles are very likely missing from the 3-T stock.

Experiment 4. Alternatively, the Gl_3 alleles of XG-15 and 3-T might be equally potent, meaning that

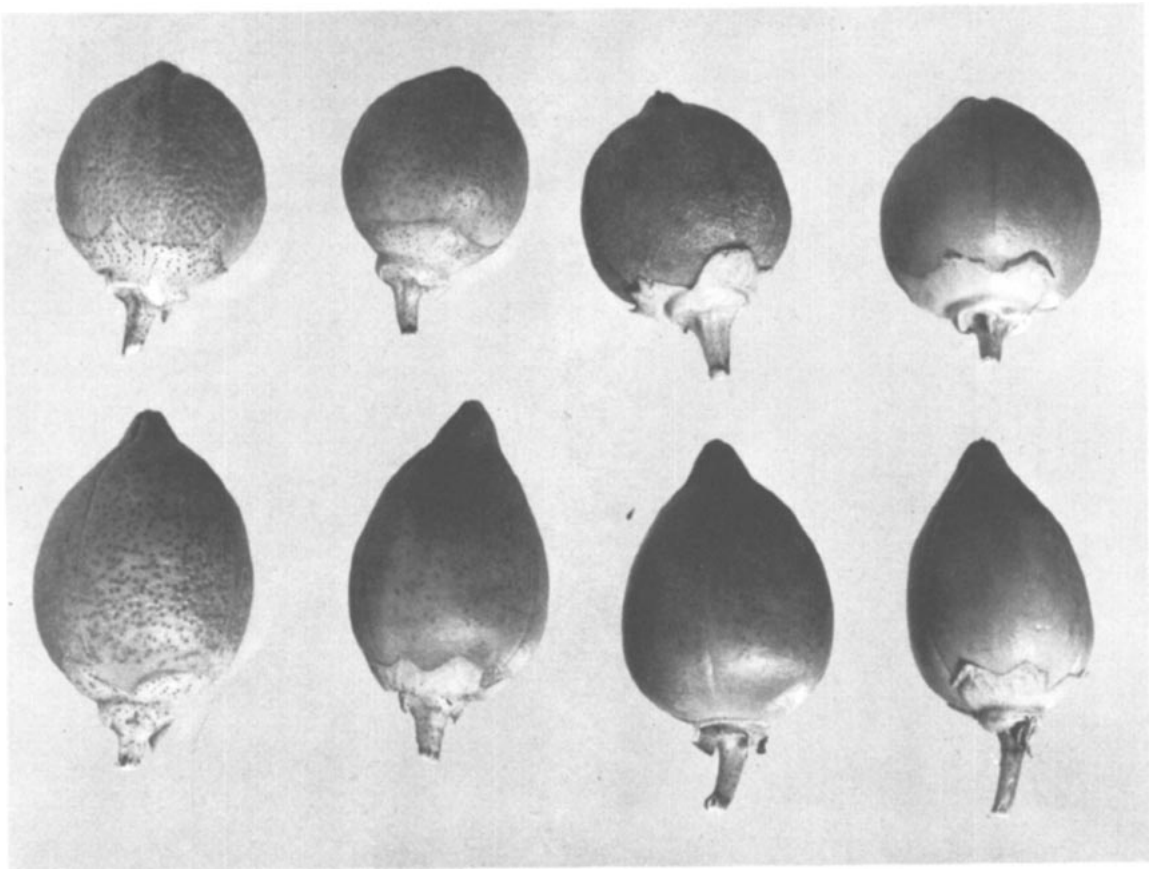

Fig. 1. Phenotypes of cotton bolls, XG-15, upper row, 3-T, lower. Genotypes from left to right: $Gl_2Gl_2Gl_3Gl_3$, $Gl_2Gl_2gl_3gl_3$, $gl_2gl_2Gl_3Gl_3$, and $gl_2gl_2gl_3gl_3$.

rugate fruit surface is the product of an interaction of such an allele with "supportive" alleles in the background. If that were the case, the Gl_3 allele in 3-T should be readily exchangeable with that of XG-15 in the production of a rugate fruit surface. An F_2 population stemming from a cross of the Gl_3 monomeric in 3-T and glandless XG-15 should include some plants with densely glanded, rugate fruits.

The F_1 of the cross had glandless bolls. None of the F_2 plants had conspicuously rugates fruits, although some had as many as 60 glands per cm^2 of boll surface.

Evidently, the Gl_3 allele in 3-T lacks the capacity to interact with alleles in the XG-15 background to impart a rugate fruit surface. Furthermore, these results suggest that the Gl_3 allele in XG-15 has primary potency for expression of the rugate character, but it must interact with other alleles for the phenoytpe to be expressed.

Experiment 5. Four backcrosses of the Gl_3 from XG-15 to glandless Pima S-4 and glandless AS-2 Sea Island followed by selfing, produced Gl_3 monomerics with densely glanded rugate bolls in both stocks. Such a fruit on AS-2 background is illustrated in Fig. 2. Introgression of the Gl_3 allele from 3-T into glandless AS-2 Sea Island produced a relatively weak grade of glandulosity in the resulting monomeric (Fig. 2).

Most stocks of *G. barbadense* usually have pitted bolls (2). Glandless forms (Fig. 2) have smooth bolls. Apparently the Gl_3 allele from XG-15 interacts with some latent genetic system in glandless AS-2 to produce a degree of fruit glandulosity and rugosity virtually equal to that of dimeric *G. barbadense*. The Gl_3 allele from 3-T displayed no such potency. These results were taken as further evidence that the Gl_3 allele in XG-15 has primary potency for the determination of rugate fruit surface. This allele might be conveniently designated Gl^r_3 for rugate carpellary surface.

Experiment 6. Gl_2 and Gl_3 monomerics of AS-2 Sea Island were crossed with glandless XG-15 and glandless 3-T. After four backcrosses of *G. barbadense* to the *G. hirsutum* stocks, monomerics were recovered and their fruits were examined. Neither allele produced densely glanded, rugate fruit surfaces in the recipient backgrounds, although the monomerics in XG-15 had bolls that were more glandular than those of their genotypic counterparts in 3-T. Apparently none of the determiners of fruit rugosity in *G. barbadense* reside at leaf gland loci.

At least two questions remain. One concerns "supportive" alleles interacting with Gl^r_3 to produce the rugate phenotype. M. J. Lukefahr selected XG-15 from a segregating population following a cross of Socorro Island Wild and the Upland cultivar, 'Deltapine 15'. I have not seen the fruits of Socorro Island Wild, but have noted that those of Deltapine 15 are smooth and not nearly as glandular as those of XG-15. About 5 years ago I recovered a segregate from the cross of

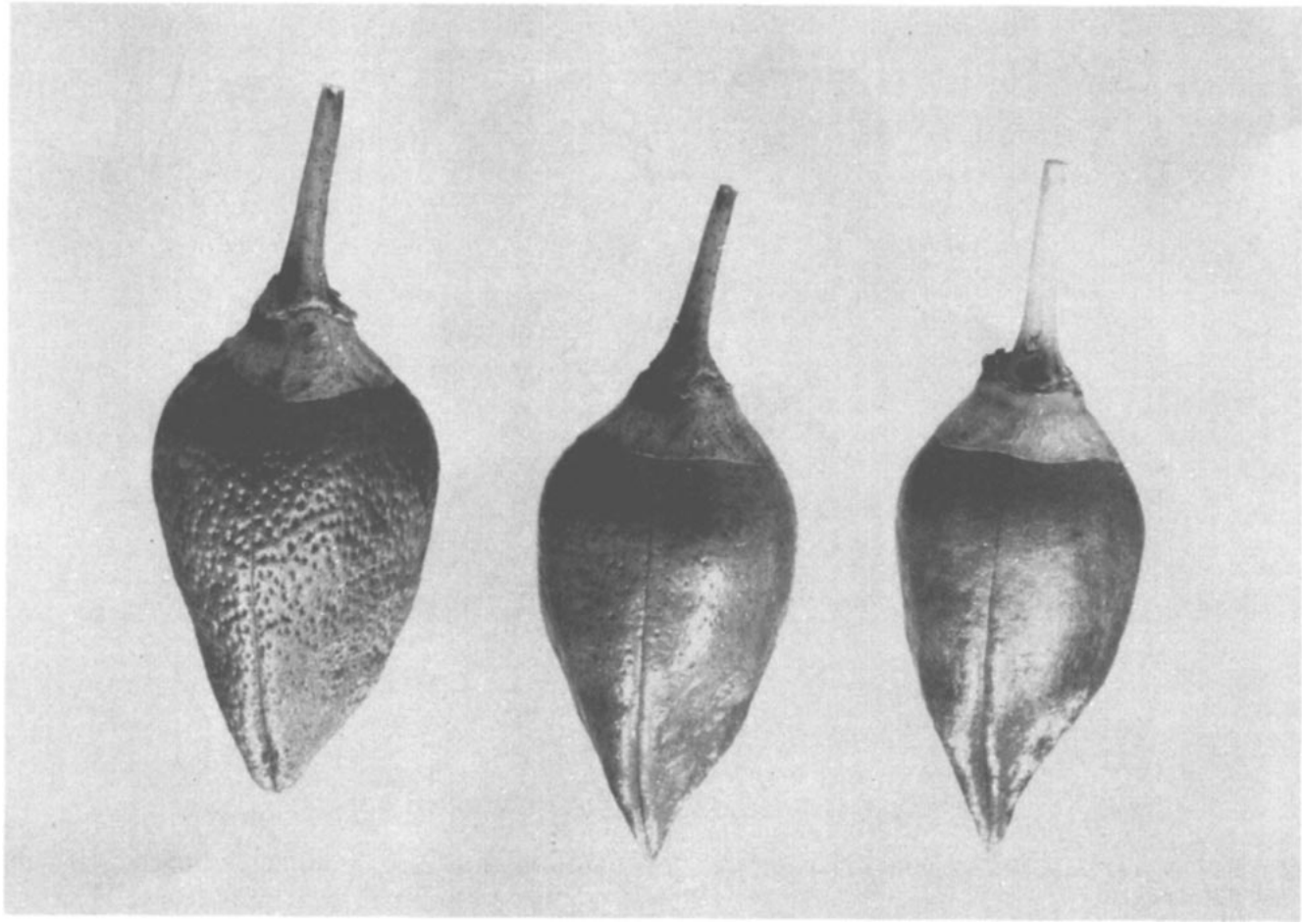

Fig. 2. Phenotypes of bolls of AS-2 Sea Island. From left to right: monomeric with Gl_3 from XG-15, monomeric with Gl_3 from 3-T, and glandless.

Deltapine 15 and Socorro Island Wild with nearly glandless bolls but with a normal level of glandulosity on other plant parts. The recovery of such a phenotype from Lukefahr's original cross leads me to believe that there was transgressive segregation for primary determiners of boll glandulosity, XG-15 being the product of one extreme and sparsely glanded boll the other. The 3-T line is probably homozygous for Gl_3, the Upland allele at the gl_3 locus, and one pair of primary boll gland determiners. The near-glandless boll character has been transferred to the upland cultivar 'Coker 310', and information on the inheritance of the trait is forthcoming.

The second question concerns the feasibility of using stocks monomeric for $Gl^r{}_3$ in programs of breeding for insect resistance. A desirable condition would be to maximize terpenoid aldehyde levels in vegetative and floral parts of the cotton plant and minimize the substances in seeds. In XG-15, the $Gl^r{}_3$ monomeric seems to give a more favorable balance of seed and flower bud terpenoids than the dimeric, the ratio being about 0.75 to 1.20% in the former as contrasted to 2.10 to 1.50 to 1.75% in the latter. Whether Upland stocks with similar levels in $Gl^r{}_3$ monomeric stocks can be bred remains to be seen.

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