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ALLELIC TESTS AMONG RAGGED LEAF, HERITABLE ABNORMALITIES 1, 2, AND 3, VEINS-FUSED, AND RUGOSE MUTANTS IN AMERICAN UPLAND COTTON, *Gossypium hirsutum* L.[1]

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ABSTRACT

Six monogenic mutants that occurred spontaneously in *Gossypium hirsutum* were tested for allelism. Allelic tests were conducted among ragged leaf and Heritable Abnormalities 1, 2, and 3 because of similar gene action. In all of these the mutant form is the heterozygote while the homozygote is semilethal. Veins-fused and rugose were included because of phenotypic similarities to Heritable Abnormalities 1 and 3, respectively. Ragged leaf and Heritable Abnormality 2 were independent of each other and of the other mutants. Heritable Abnormalities 1 and 3, veins-fused, and rugose were allelic and located at the crinkled-dwarf (*cr*) locus. Heritable abnormality 1 and veins-fused are phenotypically distinct from Heritable Abnormality 3 and rugose. This divergence of function is similar to that in the crinkled-dwarf alleles of *G. barbadense* and suggests the existence of either a complex locus or two separate loci with tight linkage.

RAGGED leaf (3) and Heritable Abnormalities 1, 2, and 3 (6) are similar in gene action. The heterozygotes are the observed mutant form and the homozygotes are semilethal. In the report on the inheritance of ragged leaf, preliminary allelic tests of ragged leaf with Heritable Abnormalities 1, 2, and 3 indicated independence of ragged leaf with these three mutants. Extensive tests of allelism among all four mutants and two additional mutants are reported in this paper.

Heritable Abnormalities 1, 2, 3 (HA1, 2, 3) and ragged leaf (*Rgrg*) are not vigorous and their use in controlled cross-pollinations was limited. Whenever possible, the mutant forms were used as pollen parents in backcrosses and testcrosses. The two additional mutants were veins-fused (4) and rugose. Veins-fused (*vfvf*) is a simply inherited recessive, but the heterozygote is identifiable in most genetic backgrounds. Rugose is a simply inherited recessive. Complete records are not available, but it is considered to be the crinkle-rugose allele (cr^1) at the crinkled-dwarf (*cr*) locus (2).

Populations for preliminary allelic tests of ragged leaf with HA1, 2, and 3 (3) were grown in 1960. Testcrosses of double heterozygotes were started in 1960, but due to the large amount of infertility, adequate seeds were not obtained for test populations, and the crosses were repeated in 1961. The F_1 (HA1 $\times$ *vfvf*) also was grown. The heterozygous mutant HA1 and homozygous *vfvf* have striking phenotypic similarities which suggest possible allelic relaitons.

The F_1 populations of (HA1 $\times$ *vfvf*) should be uniformly heterozygous *Vfvf* and should be segregating for HA1 so two phenotypes were expected, whether one assumes independent loci or allelism. In the F_1 two phenotypes appeared: a nearly normal phenotype (as expected with the *Vfvf* genotype and normal alleles from HA1) and an extreme-mutant form (Table 1). The extreme-mutant form was similar to the semilethal form of homozygous HA1, but slightly larger. The phenotypic similarities of the mutant and the extreme interaction in the F_1 suggested the possibility that the genes controlling HA1 and veins-fused could be alleles. However, the critical heterozygous form (semilethal) was sterile and could not be progeny tested.

Table 1. Tests of allelism segregation (See text for discussion).

Cross	F_1 phenotypes				F_2, BC, or TC phenotypes				
1 × 2*	0	1	2	1-2	0	1	2	1-2	
HA1 × HA2	5	5	5	4	7	11	10	11	TC
HA1 × HA3	4	6	6	4	0	19	16	0	TC
HA1 × rugose	7	13	0	0	0	14†	6	0	F_2
HA1 × vfvf	19	0	0	21‡	39	27	31§	23‡	BC^1¶
HA1 × Rgrg	0	3	4	6					
HA2 × HA3	6	4	6	2	7	4	5	7	TC
HA2 × vfvf	10	10	0	0	9	7	12	12	BC^2
HA2 × Rgrg	24	16	24	10	21	18	23	26	TC
HA3 × rugose	11	0	0	9‡	0	0	27	29	BC^2
HA3 × vfvf	10	10	0	0	0	13	27	0	BC^2
HA3 × Rgrg	19	10	16	14	38	25	56		TC
vfvf × Rgrg	10	10	0	0	14	6	7	11	BC^1

* The phenotypes are represented by numbers as follows: 0 = normal; 1 = phenotype of the first parent listed in the cross; 2 = phenotype of the second parent listed in the cross; and 1-2 = phenotype of both parents in combination. † HA1 and semilethal classes were pooled. ‡ The mutant classes represented an extreme and unexpected phenotype. § This is Vfvf. ¶ Superscript indicates backcross parent.

In 1962, backcrosses to HA1 of the *Vfvf* segregates from (HA1 $\times$ *vfvf*) and testcrosses to normal of the double heterozygotes from HA2 $\times$ *Rgrg* and HA3 $\times$ *Rgrg* were grown. HA1 $\times$ *Rgrg* was not grown because of the suspected allelism of HA1 and *vf*, and veins-fused could be used in tests with ragged leaf because of its greater fertility than HA1.

Segregation of plants in the 1962 testcrosses of ragged leaf with HA2 and HA3 indicated that it was independent of both loci (Table 1), because only two-class segregation was expected with allelism. Plants in the testcross with HA2 segregated into four classes. In the testcross with HA3, the ragged leaf phenotype was such that consistent scoring of HA3 segregation was prevented. Therefore, only three classes were scored. Plants in the backcross of the "normal" segregate (*Vfvf*) from the F_1 (HA1 $\times$ *Vfvf*) to HA1 segregated in the approximate ratio of 1 normal: 1 HA1: 1 *Vfvf*: 1 semilethal. This again suggested that HA1 and *vfvf* were alleles, but positive proof could not be established because of the inability to progeny-test the semilethal segregates.

Because of the probable allelism of HA1 and *vf* and the possibility that additional similar relationships might exist, F_1's were made in 1961 to test new combinations in 1962. The monofactorial recessive rugose was included in these tests. The F_1's (HA1 $\times$ rugose), (*vfvf* $\times$ Rgrg), and (HA3 $\times$ rugose) were grown and produced the expected two-class segregation. The F_1's (HA1 $\times$ rugose) and (*vfvf* $\times$ *Rgrg*) produced the expected phenotypes based on the parental phenotypes. However, the F_1 (HA3 $\times$ rugose) produced normal (heterozygous rugose and non-HA3) and extreme-HA3 phenotypes. The interaction of HA3 and rugose suggested possible allelic relation between the mutant genes. At this point, the data suggest the possibility of two multiple allelic series HA1-*vf* and HA3-rugose, both independent of *Rgrg*.

Additional F_1's were made to test as many combina-

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tions of the alleles as possible, and backcrosses and testcrosses of double heterozygotes from the existing F_1's were made. The F_1's (HA1 $\times$ HA2), (HA1 $\times$ HA3), (HA2 $\times$ HA3), (HA2 $\times$ *vfvf*) and (HA3 $\times$ *vfvf*) were made. [HA3 $\times$ rugose] (extreme-HA3 segregate) was backcrossed to rugose; [*vfvf* $\times$ *Rgrg*] (ragged leaf segregate) was backcrossed to *vfvf*; and [HA1 $\times$ rugose] (HA1 segregate) was self-fertilized.

The F_1 populations were grown in 1963 and exhibited no unusual segregation or phenotypes. Plants in the backcross of (HA3 $\times$ rugose) to rugose segregated into only rugose and extreme-HA3 phenotypes. The lack of recombination indicated allelism. Plants in the backcross of (*vfvf* $\times$ *Rgrg*) to *vfvf* segregated into four classes, indicating independent loci. The F_1 (HA1 $\times$ rugose) failed to segregate as expected. For example, no normal plants appeared. Three phenotypic classes were recovered, but the HA1 and semilethal classes were pooled for presentation in Table 1. The population was small (20 plants), but these data conform to the hypothesis that HA1 and rugose are alleles.

The testcrosses and backcrosses from the five F_1's were grown and scored in 1964 (Table 1). The tests of HA1, HA3, and *vfvf* with HA2 segregated into four phenotypic classes, indicating independent loci. The tests of HA1 and *vf* with HA3 resulted in only two-class segregation. Therefore, HA1, HA3, *vf* and rugose are all alleles or closely linked loci.

Rugose is apparently the crinkle-rugose allele (cr^1) at the crinked-dwarf locus (Hutchinson and Ghose, 2). Linkage tests (Kohel, Lewis and Richmond, 5) have shown that the HA1, *vf* and rugose alleles are in linkage group II (*L*°*cr Lg*), which definitely places these alleles as part of the crinkle-locus complex. The crinkled-dwarf alleles studied by Hutchinson (1) all originated in *G. barbadense,* with the exception of cr^1. The alleles reported in this paper originated independently in *G. hirsutum*. They represent slightly divergent phenotypic expressions in the HA1-*vf* and the HA3-rugose complexes. This is similar to the report of Hutchinson (1) on *G. barbadense*. This divergence of function represents either two separate loci with very tight linkage or a single locus with complex functions. Studies have been initiated to determine more precisely the nature of this allelic series.

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