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Cracked Root Mutant in Cotton: Inheritance and Linkage with Fertility Restoration[1]

J. B. Weaver, Jr. and D. B. Weaver[2]

ABSTRACT

A cracked root condition was observed in a line of upland cotton (*Gossypium hirsutum* L.) with *G. harkenssii* Brandegee cytoplasm. F_1, F_2, and testcross generations were grown to determine the inheritance of the cracked root condition. Observations indicate the character to be controlled by a single gene pair expressing complete dominance in upland stocks. In F_1 hybrids between homozygous dominant cracked root upland plants and normal root *G. barbadense* L. plants, roots appear to be normal to slightly cracked, and inheritance is uncertain. Data indicate linkage of cracked root and fertility restoration with observed recombination values ranging from 6.7 to 14.5%.

The symbol *Rc* is proposed for the gene responsible for the cracked root phenotype and the symbol *Rf* is proposed for the fertility restoring gene.

Additional index words: Fertility restorer, Cytoplasmic male-sterile, Linkage, F_1 hybrid.

IN 1977 Weaver and Weaver (2) reported a condition in upland cotton (*Gossypium hirsutum* L.) described as cracked root. The phenotype occurred in DES-HAF 16, a cytoplasmic-genetic fertility restorer strain developed by Meyer (1).

Plants expressing the cracked root character show normal root development during the first 10 days of plant growth. During subsequent plant growth until maturity, the taproot and all secondary roots develop a corkey bark-like material with fissures, hence the name cracked root. Root systems of cracked root plants appear to be less extensive and more fragile than normal root systems and tend to break easily when plants are pulled up. The character does not appear to be deleterious to above-ground portions of plants in most upland stocks when grown in nonsegregating populations. In segregating populations, the competitive ability of cracked root plants appears to be lessened in some cases. In general, plants expressing the cracked root character seem to be unaffected with regard to plant height, vegetative growth, and fruit production, although in some cases they have shorter stems and a tendency to lodge. Figure 1 shows a normal and a cracked root plant. These plants were dug from the soil because when cracked root plants are pulled up most of the lateral roots are left in the soil.

The purpose of this investigation was to determine the inheritance of the cracked root condition and to evaluate its usefulness in a breeding program. During the course of this experiment a possible linkage between cracked root and male fertility restoration was observed. Therefore, the investigation was extended to include an analysis of linkage.

MATERIALS AND METHODS

Reciprocal crosses were made during the winter of 1974-75 between plants (designated 4-811 and 4-790) expressing the cracked root phenotype and the upland cultivars 'Coker 201' and 'Delcot 277'. The strains 4-811 and 4-790 were selected from DES HAF 16 (1) after two generations of self-pollination. These two strains were considered to be "upland" types since they had been backcrossed to upland approximately seven times. F_1 progenies were planted in the 1975 summer nursery at Athens, Ga. and all plants were scored according to their expression of the cracked root phenotype. Coker 201 × 4-811 F_1 plants were self-pollinated and F_2 seeds were planted in the greenhouse. F_1's were also test-crossed as males to the upland cultivars 'Coker 310', 'Coker 304', and 'Coker 417'. These testcross progenies were planted in the 1976 nursery and scored for the cracked root character. Individual normal and cracked root plants of these testcrosses were advanced to the F_2 generation by selfing. These F_2 progenies were planted in progeny rows in the 1977 summer nursery and scored for cracked root.

Five hundred and sixty-eight F_2 plants produced by open-pollination of the F_1's 4-811 × Coker 201 (334 plants) and 4-790 × Delcot 277 (234 plants) were planted in the 1976 nursery and observed for a possible linkage of cracked root and the *G. harknessii* fertility restorer gene.

Crosses were also made between 4-790 and 'Pima S-4' (*G. barbadense* L.) and 4-811 and Pima S-4. Sixty-four F_1 plants were scored for cracked root in the 1976 nursery. F_2's obtained by selfing were planted and scored in the 1977 nursery.

Indications of linkage between cracked root and male fertility restoration suggested the need for further analysis. In 1977, randomly selected individual cracked root F_2 plants of the backcross [(Coker 201 × 4-811) × Coker 201] were testcrossed to a Coker 201 cytoplasmic male-sterile line. In 1978, the testcross progenies were scored for fertility and the racked root character.

RESULTS AND DISCUSSION

All upland × upland F_1 progenies including reciprocals (348 plants) showed full expression of the cracked root character, thus indicating the absence of cytoplasmic effects. An F_2 progeny segregated approximately three cracked roots:one normal root (Table 1). Three testcross progenies segregated approximate one cracked root:one normal root ($\chi h^2 = 4.80$, $P = 0.05$ to 0.10) (Table 1). F_2's of cracked root testcross progeny segregated 3:1 ($\chi^2 = 0.42$; Table 1.) The F_2 plants from normal root testcross progeny were all normal. Chi-square values of all families and family totals showed nonsignificant deviations from their expected ratios. Yates' correction factor (3) was used only when family populations were eight or less. These data indicate that the cracked root character is conditioned by a single gene pair expressing complete dominance in upland cotton. The symbol *Rc* is proposed for the dominant gene conditioning the cracked root phenotype.

F_1 progenies of the interspecific crosses 4-811 × Pima S-4 and 4-790 × Pima S-4 showed normal root development in 63 of 64 plants scored. One plant was judged to have a slight expression of the cracked root character. A more critical examination of these F_1

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[2] Associate prfoessor of agronomy and research assistant, Univ. of Georgia, Athens, GA 30602.

plants would probably have shown a minor expression of cracked root, because in the F_2 generation some plants showed very minor cracking of roots. F_2 progenies showed a wide range of expression. Some plants had complete expression of the cracked root phenotype but most had normal root development or only slight cracking. Of 35 F_2 plants scored (low population due to poor self seed set on F_1's), six showed full expression of the cracked root phenotype, 19 showed some fissure development, and 10 had normal roots. This ratio does not differ significantly from 1:2:1 ($\chi^2 = 0.89$, $P = 0.50$-0.75), indicating that the gene for cracked root behaves as an incomplete dominant in crosses with *G. barbadense*. The above F_2 population was also scored for fertile vs. male-sterile plants. Twenty-three of 35 plants were both male-fertile and had cracked or slightly cracked root. Seven were male-sterile with normal roots. Of the other two possible phenotypes, two were cracked root male-sterile and three were normal root male-fertile. Fertility restoration in cytoplasmic male-sterile cotton is indicated to be controlled by an incompletely dominant gene (2). Weaver and Weaver (2) failed to propose a symbol for this gene. We propose the symbol *Rf*. These data indicate linkage (14.5% recombination) between the genes for cracked root and fertility restoration.

Further evidence of linkage is found in segregating families of open-pollinated (cracked root × upland) F_2 plants. Of 568 plants scored, 273 had cracked roots and were male-fertile, while 222 were male-sterile with normal roots. Only 73 were of the nonparental or crossover types, 64 fertile and cracked root, and nine male-sterile and cracked root. These frequencies indicate a recombination value of 7.9%. However, since the F_2 plants were from open-pollinated seed, outcrosses would be expected to affect these results.

In 1978, nine testcross families were grown of the

Table 1. Segregation ratios of normal vs. cracked root cotton plants of testcross and F_2 populations at Athens, Ga., 1976 and 1977.

Cross	Cracked root	Normal	Chi-square probabilities
			(expected 3:1)
(Coker 201 × 4-811)F_2	48	18	0.50-0.75
Genotype	*Rc*	*rcrc*	
Testcross progeny			(expected 1:1)
Coker 310 × (Coker 201 × 4-811)F_1	7	11	0.20-0.50
Coker 304 × (Coker 201 × 4-811)F_1	9	6	0.25-0.50
Coker 417 × (Coker 201 × 4-811)F_1	1	7	0.05-0.10†
Total	17	24	0.25-0.50
Genotype	*Rcrc*	*rcrc*	
Cracked root testcross progeny F_2			(expected 3:1)
[Coker 310 × (Coker 201 × 4-811)]F_2	16	3	0.25-0.50
[Coker 417 × (Coker 201 × 4-811)]F_2	87	27	0.50-0.75
Total	103	30	0.50-0.75
Genotype	*Rc*	*rcrc*	
Normal root testcross progeny F_2			
[Coker 310 × (Coker 201 × 4-811)]F_2	0	50	–
[Coker 417 × (Coker 201 × 4-811)]F_2	0	23	–
Total	0	73	–

† Yate's correction factor (3) used.

Table 2. Segregation of cracked root and fertility restoring genes in a cross of *RcrcRfrf* × cytoplasmic male-sterile cotton.

Pollinator genotype	1978 Testcross families	Fertile cracked root	Sterile cracked root	Fertile normal root	Sterile normal root	Chi-square probabilities (expected 1:1:1:1)
RcrcRfrf	8-371	9	1	1	6	0.01-0.025
	8-372	14	0	1	21	<0.005
	8-373	15	0	3	16	<0.005
	8-376	18	3	0	19	<0.005
	8-380	6	0	0	2	0.005-0.01
	Total	62	4	5	64	<0.005

Fig. 1. A cotton plant with normal roots (left) compared to a plant with cracked roots.

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cross of [(Coker 201 × 4-811) × Coker 201] F_2 individual plants with cracked roots × a cytoplasmic male-sterile Coker 201. Five of the individual BC_1 F_2 plants used as pollinator parents were of the double heterozygous genotype *RcrcRfrf*. Table 2 shows the segregation ratios obtained from these five testcross families. The chi-squares test showed a highly significant deviation from the expected BC ratio. The nonparental frequencies observed indicated a recombination value of 6.7%. The other four pollinator parents had genotypes as follows: three were *RcRcRfRf* and one was *RcrcRfRf*. Therefore, all nine of the BC_1 F_2 cracked root plants used in the testcross carried the fertility restorer gene. This fact clearly indicates that the cracked root gene and the fertility restorer gene had not segregated independently. These data show close linkage between genes for fertility restoration and cracked root.

It is theorized that a small block of chromosomes from *G. harknessii* is responsible for fertility restoration in cytoplasmic male-sterile cotton. It is probable that the gene for cracked root is also located on this chromosome block. Although crossing over between the two genes occurs, restoration of fertility is better when the entire chromosome block is present. Thus, a breeder selecting for superior fertility restoration would include the cracked root trait in the selections.

Restorer lines with the cracked root character seem to be more consistently fertile and better able to restore fertility. However, in general it would be undesirable for commercial F_1 hybrids to have cracked roots. The character can be easily eliminated from breeding material. Research needs to be conducted on cracked root and its relationship to soil-borne diseases. Use of the character in this type of research may shed light upon certain host-plant relationships.

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