Heritability of Verticillium Wilt Tolerance in Crosses of American Upland Cotton[1]

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ABSTRACT

Broad-sense heritability estimates of tolerance to Verticillium wilt [*Verticillium albo-atrum* (Reinke and Berth)] under severe field exposure in American Upland cotton (*Gossypium hirsutum* L.) were compared using F_2 and F_3 generations of tolerant $\times$ susceptible crosses. Heritability estimates varied from 0 to .833, depending upon exposure level, generation tested, and type of parental tolerance present.

Tolerance to Verticillium wilt was found to be recessive for the crosses studied. Selection based on progeny row yield was effective when Verticillium wilt was severe.

Susceptible F_2 plants produced homozygous susceptible F_3 rows but progeny testing of tolerant F_2 plants was necessary to detect escapes.

Additional index words: *Gossypium hirsutum* L., Phenotypic escapes, Regression, Selection efficiency, Penetrance, *Verticillium albo-atrum* (Reinke and Berth).

VERTICILLIUM wilt, caused by the soil-borne fungus *Verticillium albo-atrum* (Reinke and Berth), was the most destructive disease of *Gossypium hirsutum* L. in 1968. Losses for that year were estimated to be 360,000 bales, or approximately $3^1/_3\%$ of the total crop (11). Damage to Upland cotton can be particularly high in irrigated regions of California, Arizona, Texas, and New Mexico.

Although cultural controls are important in reducing losses, a more feasible approach would be to plant resistant varieties. Unfortunately, at present no known sources of complete resistance have been reported in Upland cotton, and in general the varieties now in use are susceptible, with only a few containing some heritable tolerance (5).

Several problems arise when American Upland cottons are bred for Verticillium wilt tolerance. Since resistant sources, as such, are non-existent, the breeder is confronted with different levels and types of tolerance. Once the desired kind and amount of tolerance is fixed, the task of transferring it to agronomically acceptable strains remains a key obstacle.

Inheritance patterns among host species for Verticillium wilt tolerance are not consistent. In some crops inheritance appears very simple. Schaible and Denby (6, 13) concluded that resistance in tomatoes (*Lycopersicon esculentum* L.) is controlled by a single dominant gene, *Ve*; they were able to transfer resistance by backcrossing. Dominance for resistance has also been reported in strawberries (*Fragaria spp.*), potatoes (*Solanum tuberosum* L.), and sunflowers (*Helianthus annuus* L.) (10, 12, 17). Recessiveness for resistance has been shown in eggplant (*Solanum melongena*) and sunflowers (8, 12).

Inheritance of tolerance to Verticillium wilt in American Upland cotton is not well understood. Cotton (5) and Fisher (7) noted that tolerance could be transmitted to progenies only in certain crosses, while in others, transgressive segregation occurred.

Wilhelm et al. (16) have reported dominance for Verticillium wilt resistance among Upland $\times$ Sea Island crosses. Nearly true breeding lines were selected from *G. barbadense* sources, but none were found from Upland cottons. The F_1 progenies from Sea Island (resistant) $\times$ Upland (susceptible) crosses were mostly resistant, although a few were intermediate in susceptibility. Susceptible $\times$ suceptible Uplands produced susceptible progenies.

Barrow (2) also noted dominant type inheritance for resistance when a mild strain of *V. albo-atrum* was used to test tolerant $\times$ susceptible Upland crosses. Results from single crosses indicated that some heterozygosity was present within the tolerant parent, as the F_1 progenies were grouped into tolerant, susceptible, or segregating (1:1) categories.

Barnes and Staten (1) noted average effects among wide and narrow crosses with Acala parents under field conditions. Among 43 F_1 populations, 5 were more tolerant than either parent, 33 were intermediate, and 5 were more susceptible to Verticillium wilt than either parent. Tolerant $\times$ susceptible crosses generally produced susceptible F_1 plants, and mildly tolerant $\times$ susceptible crosses produced plants with intermediate reactions.

The purpose of this investigation was to estimate broad-sense heritability, and selection efficiencies of tolerant $\times$ susceptible *Gossypium hirsutum* populations under severe field conditions.

MATERIAL AND METHODS

From 1966 to 1968 the following populations of American Upland cottons were evaluated at Las Cruces, N. M.:

1. 8229 Verticillium wilt-tolerant parent (T)
2. 8076 Verticillium wilt-tolerant parent (T)
3. 8861 Verticillium wilt-tolerant parent (T)
4. Lankart 57 Verticillium wilt-susceptible parent (S)
5. 8229 $\times$ Lankart 57 F_2 and F_3
6. 8076 $\times$ Lankart 57 F_2 and F_3
7. 8861 $\times$ Lankart 57 (reciprocal matings) F_1, F_2 and F_3

Populations 1, 2, and 3 are Verticillium wilt-tolerant Upland strains developed by the New Mexico Experiment Station and were chosen as parents because of their superior performance in several replicated yield tests on wilt-infested soils. Population 4 was chosen to represent sensitivity to verticillium wilt under southern New Mexico conditions.

The F_1 and F_2 nurseries consisted of single-row entries, 100 feet and 325 feet long, respectively, with the inclusion of the parents on adjacent rows of equal length. Within-row spacings was approximately three plants per meter. All F_1 plants were utilized except for end plants. One hundred-fifty plants from each F_2 and parent were randomly selected and tagged as the experimental unit. Random selections were made at harvest from the F_2 and parental pools for progeny tests the following year.

Design of the F_3 progeny test was completely random, with each entry adjacent to a progeny from a randomly selected parental "check" plant. Plots were 20 feet long with 1.5-m (5-foot) alleys. Environmental conditions were favorable for Verticillium wilt expression, and natural infection was uniform throughout the experiments.

Wilt damage to single plants and progeny rows was graded periodically throughout the season, using five phenotypic grades based on defoliation; grade 1 denoted 0 to 20% defoliation, and grade 5 denoted complete defoliation.

Broad-sense heritability estimates for tolerance to Verticillium wilt and seed cotton yields were calculated using: (i) variance F_2 — variance pooled parents ÷ variance F_2 (3, 9, 14) and (ii) variance F_3 progeny rows — variance pooled parents ÷ variance F_3 progeny rows (9, 14). Average variance of the parents was used to estimate environmental effects.

RESULTS AND DISCUSSION

Heritability Estimates: Crosses with Common Susceptibles

Broad-sense heritability estimates of disease tolerance indicated that different patterns existed among crosses, generations, and exposure levels (Tables 1 and 2).

Good genotype-phenotype relationships were obtained within the 8076 × Lankart populations. Estimates varied from .254 to .586 for the F_2's and .128 to .730 for F_3 progenies. Heritability estimates increased with exposure levels for both generations, and the variaitons were significant for gradings after the 1st week in August.

Heritability estimates were substantially lower within the 8229 × Lankart 57 populations, ranging from .071 to .401 for F_2's and .147 to .374 for F_3 progenies. Estimates for this cross declined with increasing exposures, and the variances were generally nonsignificant.

Heritability estimates from F_3 progeny rows were higher in both crosses than estimates from F_2's because some individual plants were phenotypic escapes, and were not detected until progeny tested.

Because both crosses had a common susceptible parent (Lankart 57), it was assumed that the differences noted were due to genetic differences between the 8076 and 8229 parental strains. The 8076 strain retained its leaves under severe exposures to $V.$ *albo-atrum*. In contrast, the 8229 strain expressed tolerance by replacing damaged leaves at each node, giving a regrowth appearance that was difficult to measure.

Under severe exposure levels, seed cotton yields produced higher estimates of heritability than those from disease ratings. Estimates based on F_2 data, however, were not indicative of progeny row estimates. The differences obtained between generations were probably due to the experimental unit. Single F_2 plants were more likely to escape infection, even though conditions were ideal, than were their subsequent progeny rows.

Probability of Selecting Tolerant Progeny Rows

Regression of progeny wilt grades on F_2 plants grades at maximum exposure indicated that heritability estimates were much lower than by previous methods (Tables 3 and 4). These estimates of .236 and .082 for the crosses 8076 × Lankart 57 and 8229 × Lankart 57, respectively, were lower primarily because an estimated 10% of the F_2 plants escaped visual injury and were not detected as susceptible until progeny tested.

Selection efficiencies for the cross 8076 × Lankart 57 were fairly high, which indicated that a considera-

Table 1. Summary of heritability estimates from F_2 and F_3 generations associated with Verticillium wilt damage from the cross 8076 × Lankart 57.

Date	F_2 plant		F_3 progeny	
	σ^2	$h^{2\dagger}$	σ^2	$h^{2\ddagger}$
Visual grading:				
8-3	.423	<.000	.647	.128
9-12	1.931**	.280	1.582**	.633
9-20	2.315**	.254	1.397**	.712
9-27	1.870**	.348	1.441**	.730
10-13	.724**	.586	.648**	.677
Yield-seed cotton:	1859.548	.362	1.062**	.833

** Significantly different from pooled parents at .01 level.
† Where $h^2 = (\sigma^2 F_2$ plants $- \sigma^2$ Pooled parents$)/\sigma^2 F_2$ plants.
‡ Where $h^2 = (\sigma^2 F_3$ Progeny $- \sigma^2$ Pooled parents$)/\sigma^2 F_3$ progeny.

Table 2. Summary of heritability estimates from F_2 and F_3 generations associated with Verticillium wilt damage from the cross 8229 × Lankart 57.

Date	F_2 plant		F_3 progeny	
	σ^2	$h^{2\dagger}$	σ^2	$h^{2\ddagger}$
8-3	.955**	.401	.618	.282
9-12	1.946	.139	.638	<.000
9-20	2.054	.071	.589*	.374
9-27	1.733	.155	.505	.244
10-13	.369	<.000	.139	.147
Yield-seed cotton:	2989.958**	.593	.452*	.367

* Significantly different from pooled parents at .05 level.
** Significantly different from pooled parents at .01 level.
† Where $h^2 = (\sigma^2 F_2$ plants $- \sigma^2$ Pooled parents$)/\sigma^2 F_2$ plants.
‡ Where $h^2 = (\sigma^2 F_3$ Progeny $- \sigma^2$ Pooled parents$)/\sigma^2 F_3$ progeny.

Table 3. Relationship of tolerance of F_3 progeny rows to tolerance of the parental F_2 plant from the cross 8076 × Lankart 57†.

Wilt grade of parental F_2 plants	Number of F_3 progeny rows in wilt grade					Mean grade	Selection efficiency index‡
	1	2	3	4	5		
1	1	4	4	5	10	3.8	21
2	2	2	2	3	6	3.6	27
3	0	1	0	1	4	4.3	17
4	0	1	1	7	10	4.4	5
5	0	0	0	2	5	4.7	0

* Significantly different from pooled parents at .05 level.   † F_2's were graded 9-6-66 and F_3 progenies on 9-27-67. Regression and correlation coefficients were .236 and .283* respectively.   ‡ The percentage probability of selecting an F_3 progeny row with a grade of 1 or 2. Grade 1 tolerant, Grade 5 defoliated.

Table 4. Relationships of tolerance of F_3 progeny rows to tolerance of the parental F_2 plant from the cross 8229 × Lankart 57†.

Wilt grade of parental F_2 plants	Number of F_3 progeny rows in wilt grade					Mean grade	Selection efficiency index‡
	1	2	3	4	5		
1	0	0	6	5	20	4.4	0
2	0	0	1	1	6	4.6	0
3	0	0	1	4	6	4.5	0
4	0	0	0	3	11	4.8	0
5	0	0	0	2	6	4.8	0

† F_2's were graded 9-6-66 and F_3 progenies on 9-27-67. Regression and correlation coefficients were .082 and .177 n. s. respectively.
‡ The percentage probability of selecting an F_3 progeny row with a grade of 1 or 2. Grade 1 tolerant, Grade 5 defoliated.

ble amount of gain could be made by selection (Table 3). If plants showing no symptoms or those with minor chlorosis (grades 1 and 2) were considered as tolerant, then approximately 16% F_3 progenies were recovered as tolerant to Verticillium wilt.

Selection efficiencies, in comparison, were 0 for the cross 8229 × Lankart 57, as none of the F_2 plants produced any tolerant (grade 1 or 2) F_3 progenies (Table 4). Only eight of the 72 progenies were rated as intermediate in disease severity. Approximately 91% of the F_3's were susceptible for this cross.

All F_2 plants, in both crosses, that were completely defoliated (grade 5) were homozygous for susceptibil-

Table 5. Phenotypic correlation and regression coefficients of Verticillium wilt grades (9/12) and seed cotton yields.

Population	Correlation between grade & yield	Regression yield on wilt†	Mean wilt grade‡	Mean yield (kg)
8229 Parent	-.553**	-.19	2.50	1.26
8076 Parent	-.387	-.11	2.17	1.31
Lankart 57 Parent	-.197	-.05	4.70	.23
8076 × Lankart 57 F₃	-.704**	-.20	3.30	.93
8229 × Lankart 57 F₃	-.480**	-.17	3.81	.82

** Significant at .01 level. † Kilograms/plot. ‡ Grades 1 to 5. Grade 1 - tolerant, Grade 5 - defoliated.

Table 6. Broad-sense heritability estimates and variances for Verticillium wilt damage in a reciprocal F₂ generation.

Date	8861 (male) × Lankart 57 (female)		Lankart 57 (male) × 8861 (female)	
	σ^2	h^2†	σ^2	h^2
Wilt grades:				
8-3	1.089	<.000	1.162	<.000
8-10	1.716	.117	1.548	<.000
8-21	2.188**	.400	2.100**	.497
8-31	2.010	.165	2.189	.360
9-11	1.537	.185	1.795	.212
9-19	1.229	.146	1.159	.174
Yield-seed cotton:	1110.080	.179	1360.590**	.618

² Significant at .05 level. ²² Significant at .01 level. $+ h^2 (\sigma^2 F_2 - \sigma^2 F_1)/\sigma^2 F_2$

Table 7. Variances and broad sense heritability estimates for Verticillium wilt damage in a reciprocal F₃ progeny test.

Date	8861 (male) × Lankart 57 (female)		Lankart 57 (male) × 8861 (female)	
	σ^2	h^2†	σ^2	h^2
Wilt grades:				
8-13	.733*	.480	.843*	.459
9-5	1.200*	.440	.855*	.408
9-16	.724*	.458	.438	.261
9-26	.401	.244	.253	<.000
Yield-seed cotton:	.191**	.541	.139	.304

* Significant at .05 level. ** Significant at .01 level.
† $h^2 (\sigma^2 F_3 progeny - \sigma^2$ Pooled parent)$/\sigma^2 F_3$ progeny.

Table 8. Frequency distribution (%) of plant Verticillium wilt grades in a reciprocal F₁ and F₂ generation.

	Wilt grades					Average wilt grade
	Tolerant			Susceptible		
	1	2	3	4	5	
8861						
Parent (T)	18.0	17.9	24.5	33.0	6.6	2.92
Lankart 57						
Parent (S)	6.6	0.9	2.8	16.1	73.6	4.49
Tol. parent as male						
F₁	5.2	1.0	5.2	10.4	78.2	4.55
F₂	4.7	4.7	6.7	9.3	74.7	4.45
Tol. parent as female						
F₁	4.8		4.8	14.3	76.2	4.57
F₂	5.3	2.0	7.3	15.3	70.0	4.43

ity. The number of tolerant F₃ progenies recovered from the crosses corresponded well with the heritability estimates obtained. It would seem advisable (within wide crosses such as those used) to select a large number of F₂'s and to progeny test those plants that showed a tolerant or moderately tolerant reaction. If a limited number of F₂'s were selected, then the possibility would exist for missing tolerant material, especially within crosses of low penetrance. Considerable gain in wilt tolerance *per se* could be made, although a large number of tolerant F₃ rows would be lost to other agronomic considerations such as plant size, maturity, and fiber properties.

Correlation of Wilt Damage and Yield

Significant negative correlations between disease ratings and seed cotton yields were obtained from both F₃ populations and the parental strain 8229 (Table 5). Severity-yield correlations were not significant for Lankart 57 and the 8076 parents. Three-fourths of all Lankart 57 plots were completely defoliated, producing little variation in wilt grades or yields. All entries from the 8076 strain were rated as tolerant or moderately tolerant (grades 1, 2 or 3), which also reduced wilt grade and yield variations.

Heritability Estimates: Reciprocal Crosses

Broad-sense heritability estimates from the reciprocal cross 8861 (tolerant) × Lankart 57 (susceptible) were inconsistent generation to generation. Heritability estimates based on F₁ and F₂ data (Table 6) were lower when the tolerant parent was the pollen source and conversely higher when F₃ progenies were considered (Table 7). Estimates decreased with increasing exposure levels after mid-August, when symptom expressions were optimum. Again, as was experienced with earlier crosses, estimates based on early generations were not indicative of progeny row estimates.

Frequency distribution and means of parents and F₂ progenies indicated tolerance to be highly recessive for the reciprocal cross 8861 × Lankart 57 (Ta-

ble 8). Both F₁ populations equalled the Lankart parent in susceptibility, and the F₂'s approached the susceptible parent. Maternal effects for wilt tolerance were not noted.

In mid-September, when wilt symptoms were maximum, the Lankart 57 parent had approximately 10% tolerant and moderately tolerant plants (grades 1, 2, and 3). If this parent is assumed to be homozygously susceptible (as revealed by subsequent progeny testing), and the tolerant plants are "escapes," then the F₁'s can be estimated as essentially 100% susceptible. By using the susceptible parent to measure the "escapes," the effective tolerance (grades 1, 2, and 3) within F₂'s is about 5%. The possibility then exists for double homozygous recessive genes conditioning Verticillium wilt tolerance under these conditions (4).

REFERENCES

1. Barnes, Carl E., and Glen Staten. 1961. The combining ability of some varieties and strains of Gossypium hirsutum. N. Mex. Agr. Exp. Sta. Bull. 457.
2. Barrow, J. R. 1970. Heterozygosity in inheritance of Verticillium wilt tolerance in cotton. Phytopathology 60:301-303.
3. Burton, G. W., and E. H. Devane. 1953. Estimating heritability in tall fescue (Festuca arundinacea) from replicated clonal material. Agron. J. 45:478-482.
4. Castle, W. E., and S. Wright. 1921. A method of estimating the number of genetic factors in cases of blending inheritance. Science N.S. 54:223.
5. Cotton, John R. 1965. Breeding cotton for tolerance to Verticillium wilt. USDA Agr. Res. Ser. Bull. 34-80.
6. Denby, L. G., and G. E. Woolliams. 1962. The development of Verticillium-resistant strains of established tomato varieties. Can. J. Plant Sci. 42:681-685.
7. Fisher, Warner D. 1968. Breeding cotton for tolerance to Verticillium wilt. Beltwide Cot. Prod. Res. Conf. Proc. p. 230.
8. Lockwood, J. L., and D. Markarian. 1961. Breeding eggplants for resistance to Verticillium wilt. Quart. Bull. Mich. Agr. Exp. Sta. 44:15-20.
9. Lush, J. L. 1949. Heritability of quantitative characters in farm animals. Proc. Eighth Int. Cong. Genetics. 1948. Hereditas Suppl. 356-375.

10. McLean, J. G. 1955. Selecting and breeding potatoes for field resistance to Verticillium wilt in Idaho. Idaho Agr. Exp. Sta. Res. Bull. 30.

11. Motsinger, Ralph E. 1969. Report of the cotton disease loss estimate committee. Beltwide Cot. Prod. Res. Conf. Proc. p. 4.

12. Putt, E. D. 1954. Breeding behavior of resistance to leaf mottle on Verticillium wilt in sunflowers. Crop Sci. 4:177-179.

13. Schaible, Lester, O. S. Cannon, and V. Waddoups. 1951. Inheritance of resistance to Verticillium wilt in a tomato cross. Phytopathology 41:986-990.

14. Self, F. W., and M. T. Henderson. 1954. Inheritance of fiber strength in a cross between the Upland cotton varieties AHA 50 and Half and Half. Agron. J. 46:151-154.

15. Weber, C. R., and B. R. Moorthy. 1952. Heritable and non-heritable relationships and variability of oil content and agronomic characters in the F_3 generation of soybean crosses. Agron. J. 44:202-208.

16. Wilhelm, Stephen, James E. Sagen, and Helga Tritz. 1969. Dominance of Sea Island Resistance to Verticillium wilt in F_1 progenies of Upland $\times$ Sea Island cotton crosses. Beltwide Cot. Res. Conf. Proc. p. 31. (Abstr.)

17. —————. 1955. Verticillium wilt of strawberry with special reference to resistance. Phytopathology 45:387-391.