

A Quantitative Genetic Study of Verticillium Wilt Resistance Among Selected Lines of Upland Cotton¹

Laval M. Verhalen, L. A. Brinkerhoff, Kwee-Chong Fun,
and Walter C. Morrison²

ABSTRACT

A quantitative genetic study of the inheritance of resistance to verticillium wilt (*Verticillium albo-atrum* Reinke and Berth.) was conducted among 10 selected lines of upland cotton (*Gossypium hirsutum* L.) utilizing the Jinks-Hayman diallel analysis. Parents and F₁'s were studied in 1968 and 1969 at two locations in Oklahoma with the inclusion of F₂ progenies in the second year.

General tests of the diallel assumptions revealed a partial noncompliance with those assumptions in this material. Epistasis did not appear to be a complicating factor herein, but significant genotype by environment interactions were found among parents from year to year for their additive and dominance components of variation. A significant portion of the dominance interactions could not be attributed to either years or locations.

All estimates of environmental variance and of additive genetic variance were significant, as were most estimates of dominance genetic variance. With one exception, estimates of additive variance were larger than the other parameters estimated in the same test. Wilt resistance displayed partial dominance except in one environment where overdominance was found to occur. Direction of dominance was toward greater susceptibility. The frequency of negative versus positive alleles in the parents was likely unequal and biased towards greater susceptibility. Narrow-sense heritability estimates suggested that rapid genetic advances through selection could be made in most environments.

Additional index words: Visual grades, *Verticillium albo-atrum* Reinke and Berth., *Gossypium hirsutum* L., Diallel analysis, Epistasis, Genotype by environment interaction, Dominance, Heritability.

VERTICILLIUM wilt (*Verticillium albo-atrum* Reinke and Berth.) has become one of the most serious diseases of upland cotton (*Gossypium hirsutum* L.) in Oklahoma, particularly under irrigated production. The disease appears to be more widespread throughout the state than it was in the recent past, and it seems to be increasing in severity within areas of previous infestation.

Cultural practices can partially alleviate the intensity of verticillium wilt (10, 20); but as with other plant diseases, most effective and economical control should be obtained through use of highly tolerant or resistant varieties (20). Cotton breeders have been working toward this objective for many years, and considerable progress has been made in developing upland varieties possessing a fair degree of tolerance to the disease (7, 10, 20, 21). However, commercial upland varieties resistant to verticillium wilt

¹ Journal Article 2111 of the Agricultural Experiment Station, Oklahoma State University, Stillwater, Okla. Research conducted by the Departments of Agronomy and of Botany and Plant Pathology in cooperation with the Crops Research Division, A.R.S., U.S.D.A. Received November 2, 1970.

² Assistant Professor (Dept. of Agronomy); Plant Pathologist (Crops Research Division, A.R.S., U.S.D.A.) and Professor (Dept. of Botany and Plant Pathology); Graduate Student (Dept. of Agronomy); and Graduate Research Assistant (Dept. of Agronomy), respectively. Oklahoma State University, Stillwater, Okla. 74074.

have not yet been developed. Progress has been made in spite of the fact that the genetics of resistance to verticillium wilt in upland cotton are largely unknown. Should this genetic basis be defined, it is probable that more rapid progress toward varietal resistance would be achieved.

The research reported herein was undertaken to determine the inheritance of resistance to verticillium wilt among 10 selected lines of upland cotton.

LITERATURE REVIEW

Wilhelm, Sagen, and Tietz (23) reported that the F_1 's of 56 different crosses between verticillium wilt-resistant *Gossypium barbadense* L. and susceptible *G. hirsutum* were predominantly resistant but that some intermediate plants also occurred. First generation backcrosses of seven F_1 's to their resistant parents again produced resistant plants with an occasional slightly less resistant individual. Backcrosses of 12 F_1 's to their susceptible parents yielded resistant, intermediate, and susceptible plants. They concluded that resistance in such crosses was determined by a single dominant (or partially dominant) factor. Subsequent research (24) in a cross between 'Seabrook' (*G. barbadense*) and 'Rex' (*G. hirsutum*) produced an F_1 which was intermediate in resistance and revealed segregation ratios in the F_2 which approximated 3 resistant:1 susceptible, in the backcross between the F_1 and Rex of 0:1, and in the backcross between the F_1 and Seabrook of 1:0. The backcross ratios certainly suggest a genetic background effect. Different degrees of resistance and susceptibility were noted which could also suggest a genetic background effect or a gene of variable expressivity.

Bell and Presley (4) concluded that resistance was transferred as a dominant character in the F_1 's between a resistant *G. barbadense* and seven susceptible *G. hirsutum* varieties. Two of the crosses displayed partial dominance while five exhibited complete dominance. Screening was accomplished using the D (defoliating) strain of the pathogen, and it was effective only under particular temperature regimes.

Barrow (3), also using a specific temperature regime but using the SS-4 isolate of the pathogen, obtained tolerant F_1 's in a cross between 'Acala 9519' (tolerant *G. hirsutum*) and 'Acala 227' (susceptible *G. hirsutum*), an approximate 3:1 ratio of tolerants to susceptibles in the F_2 , and a 1:1 ratio in the first backcross of the F_1 to its susceptible parent. These facts support a hypothesis of a single dominant gene difference between these two lines for tolerance to SS-4. The T-1 isolate produced symptoms too severe for accurate differentiation between these two parental types.

Stith (21), in reasoning from Mendelian segregation ratios and laws of probability, concluded that the inheritance of resistance to verticillium wilt within *G. hirsutum* was a quantitative, rather than a qualitative character.

MATERIALS AND METHODS

Ten populations of upland cotton, four of which were released varieties, were used as parents in this experiment. One of the 10, 'Stoneville 62', was included as a complete susceptible while the other nine were selected to sample different degrees of tolerance to the disease. The parents, their pedigrees, and

Table 1. Parents used in the study; their pedigrees and mean verticillium wilt grades.

Parents	Pedigrees	Mean verticillium wilt grades over locations†	
		1968	1969
M66-068	[(B ₂ B ₃ B ₄ × L. 57) × L. 57] × DPL 5540 F ₉	6.4	6.0
M66-067	(L. 611 × Fox 42-5) × Fox 42-5 F ₃	5.9	5.3
M66-076	[(3060 × L. 57) × L. 57] × DPL 5540 F ₃	6.0	5.2
OK 141-5	Sel. from 62 NM 8060-3 (2503 × Coquette F ₇)	2.6	2.9
Mo-Del	-----	5.9	6.0
Stoneville 7A	-----	6.4	5.4
Westburn	-----	6.6	7.3
67-40A-409	Im 2-1-6 × Acala 44 F ₃ 411-10	5.6	5.2
832-B	Sel. from Lankart 57	6.4	5.6
Stoneville 62	-----	7.5	8.2

* See Table 2 for verticillium wilt grades and their corresponding adult plant symptoms.

† Since a significant years × parents interaction was obtained for this trait (see Table 5), the means for each year over the Stillwater and Altus locations are listed separately.

mean disease grades are presented in Table 1. Since the parents were specifically chosen, inferences derived from the data apply only to the material studied. The extent to which they apply to *G. hirsutum* as a whole is unknown.

Crosses among the 10 parents were made in all possible combinations (ignoring reciprocals) at Iguale, Mexico, in the winter of 1967-68. In 1968 and 1969, the 10 parents and the 45 F_1 crosses among them were planted in a randomized complete block design with four replications at Altus and Stillwater, Okla. In 1969, the 45 F_2 progenies were also included. Plots were single rows 7.6 m long; rows were 1.0 m apart; and individual plants within rows were spaced at a distance of approximately 0.3 m, except at Altus in 1968 where adjacent hills were 0.2 to 0.3 m apart with one to four plants/hill. In each test a check row of 'Kemp' (highly susceptible) and one of 'Stoneville 7A' (fairly tolerant) were planted between each fourth and fifth plot. Both test locations were on clay soils which had continuous histories of heavy verticillium wilt infestation for several years, and both received supplemental irrigation.

Attempts were made at each location in each year to evaluate resistance in juvenile plants by inoculating alternate plants in the row during the latter part of June and early July. However, high temperatures following inoculations apparently inhibited disease development. All plants were then reinoculated in early September except in the Altus test in 1968. In that test, natural infection was of such severity that reinoculation was judged unnecessary. A hypodermic needle inoculation technique (5, 6) was used in 1968 while in 1969 a needle and sponge puncture method (S. Evans, 1949. Greenhouse tests of methods used in the inoculation of cotton plants with *Verticillium albo-atrum*. M.S. Thesis. Oklahoma State University, Stillwater) was employed. For both methods, a small drop of a suspension of *Verticillium albo-atrum* containing approximately 1×10^6 conidia/ml was placed in the cambial region of the main stem. Plots were heavily irrigated about mid-September, some two to three weeks later than normal at those locations. Comparative disease development in adjacent irrigated versus non-irrigated plots strongly suggested that the late irrigation materially increased wilt severity.

Plants were graded by visual inspection of gross external symptoms and of vascular discoloration in cut stems of those plants without external symptoms. As shown in Table 2, the grading scale ranged from one to 10. Since this work was completed, a question has arisen regarding the use of vascular discoloration as one criterion in our differentiation between grades one and two. Fisher and Blank (W. D. Fisher, personal communication, 1970) in Arizona have found nearly 100% stalk discoloration under moderate to severe wilt infection. Plants with no discoloration in those circumstances have invariably been escapes. The degree of discoloration has been variable, and its correlation with external wilt symptom ratings has been erratic. Under mild wilt expression where leaf symptoms were inconspicuous or absent, 75 to 100% of discolored stalks were found in tolerant lines whereas 0 to 30% were found in lines considered susceptible. One point that may be of consequence here is that many of their tolerant lines were derived from similar genetic materials. J. R. Barrow (personal communication, 1970) in New Mexico has found severe stem discoloration in some of his most tolerant as well as most susceptible strains. He cites unpublished data of C. Roberts which only rarely gave significant correlations between stem and foliage grades. As a consequence, some ambiguity may exist between our grades one and two. However, since 98% of the plants in this experiment were assigned grades

Table 2. Verticillium wilt grades and their corresponding adult plant symptoms.

Grades	Adult plant symptoms
1	No visible leaf symptoms; no vascular discoloration in stems
2	Very mild leaf symptoms or vascular discoloration in stems
3	Moderate leaf symptoms
4	Severe leaf symptoms; little defoliation
5	Approximately 50% defoliated
6	Approximately 75% defoliated; often plants dwarfed
7	Approximately 90% defoliated; terminals of side branches last to shed
8	Nearly defoliated; often some regrowth from lower part of plant
9	Defoliated; stems dying back but alive at ground level
10	Defoliated; stems dead down to ground level

from two through 10, the bias this ambiguity (if present) introduces into the data was considered negligible.

Disease readings were taken on an individual plant basis in the first two weeks of October on 10 consecutive plants within each plot. The first plant in each plot was not graded because of possible border effects. One replication at Stillwater in 1969 was discarded because infection was not present in the susceptible check rows over much of that block.

Grades were analyzed using the diallel cross analysis proposed by Jinks and Hayman (11, 16, 17). By conducting this sort of analysis, quantitative rather than qualitative inheritance was assumed for wilt resistance in this material.

RESULTS AND THEIR IMPLICATIONS

Analyses of variance were conducted on a plot mean basis for the data from each location in each year. Significant differences among entries at the 0.01 probability level were obtained in each analysis. Diallel analyses were then conducted at each location on three sets of data, i.e., the F_1 (and parental) data in 1968, F_1 (and parental) data in 1969, and F_2 (and parental) data in 1969.

General Tests of the Assumptions

Assumptions of the diallel analysis include homozygous parents, diploid segregation, no reciprocal differences, no multiple alleles, uncorrelated gene distributions, no epistasis, and no genotype-environment interactions within locations and years (8). Failure of any one or any combination of those assumptions invalidates, to some degree, the inferences derived by means of the analysis. Therefore, three general tests were employed to examine compliance with the assumptions as a whole.

The first general test of the assumptions is an analysis of variance of the quantity $(W_r - V_r)$ where W_r is the covariance of the members of the r th array with their nonrecurrent parents, V_r is the variance of the members of the r th array, and the r th array includes the r th parent as well as all the crosses in which it is involved. If the assumptions are valid, $(W_r - V_r)$ is expected to be constant over arrays (11, 14, 17). The quantity was obtained for each array in each replication, and analyses of variance were conducted on the 40 values obtained within each set of data. At Stillwater in 1969 only three replications, thus 30 values, were available. As shown in Table 3, the arrays mean squares were not significant at the 0.05 probability level in any set of data. The results of this test therefore imply that wilt resistance in this material fulfills the assumptions of the analysis.

The second test is an analysis of the (W_r, W_r') linear regression where W_r' is the covariance of the members of the r th array with the array means of their nonrecurrent parents and where W_r is as previously defined. In this test the regression coefficients

Table 3. Analyses of variance of $(W_r - V_r)$ values.

Sources	df†	Mean squares					
		Altus			Stillwater		
		F_1 (1968)	F_1 (1969)	F_2 (1969)	F_1 (1968)	F_1 (1969)	F_2 (1969)
Arrays	9 (9)	.3421	.0900	.1075	.2287	.2515	.1992
Replications	3 (2)	.3919	.5018**	.0402	.0810	.0940	1.0449
Error	27 (18)	.3782	.1060	.0866	.1480	.3438	.9641

*, ** Significant at the 0.05 and 0.01 levels of probability, respectively. † Numbers in parentheses denote the degrees of freedom in the Stillwater 1969 F_1 and F_2 analyses.

Table 4. (W_r, W_r') and (V_r, W_r) regression coefficients and their 95% confidence limits.

Locations	Generations	(W_r, W_r')		(V_r, W_r)	
		Coef- ficients	95% confidence limits	Coef- ficients	95% confidence limits
Altus	F_1 (1968)	.171	(-.087)–.429	.511	(-.131)–1.153
	F_1 (1969)	.199	(-.106)–.504	.749	.222–1.276
	F_2 (1969)	.565	.355–.775	.631	.222–1.040
Stillwater	F_1 (1968)	.328	.248–.408	.727	.149–1.305
	F_1 (1969)	.285	.184–.386	.740	.223–1.257
	F_2 (1969)	.350	(-.224)–.924	.536	.200–0.872

should be significantly different from zero but not from 0.5 if the trait complies with the assumptions of the analysis (1). Mean estimates of W_r and W_r' for each array over replications were obtained, and regression coefficients were then calculated within each set of data. The coefficients and their 95% confidence limits are presented in Table 4. Only one set of data (Altus, 1969, F_2) fulfilled both expectations of the test while another (Altus, 1968, F_1) failed both. The remaining sets either included zero in the confidence interval or did not include 0.5. This test suggests at least a partial failure of the assumptions.

The third general test is an analysis of the (V_r, W_r) linear regression where V_r and W_r are as previously defined. The coefficients in this test should be significantly different from zero but not from 1.0 if the assumptions are valid (17). Mean estimates of V_r and W_r and their regressions were calculated in the same manner as in the previous test. The coefficients and their 95% confidence limits may be found in Table 4. Only one interval (Altus, 1968, F_1) included zero, and only one (Stillwater, 1969, F_2) failed to include 1.0. Except for the two partial failures, results of this test complied with expectations.

Summarizing the general tests of the assumptions, three tests were conducted on three sets of data from two locations. Of those 18 tests, a complete failure was obtained in only one instance while six partial failures were noted. Those failures prevent one from stating categorically that the trait fulfilled the assumptions of the analysis, but the greater frequency of successes leads one to conclude that such failures as were present were relatively minor.

Tests of Specific Assumptions

Two specific assumptions were tested, namely those of no epistasis and of no genotype-environment interactions within locations and years. Epistasis was investigated via the chi-square test formulated by Hayman (12). Since parental, F_1 , and F_2 data are required for this test, it could be utilized only on the 1969 data. Observed chi-square values with 45 degrees of freedom were 21.0 at Altus and 30.0 at Stillwater. Neither value was significant at the 0.05 probability level. Therefore, epistasis was not a contributing fac-

tor to the partial failures of the assumptions noted above.

The assumption of no genotype-environment interactions within locations and years was tested using the analyses proposed by Allard (2) for the additive and dominance components of variation. The test for the additive components is based on the assumption that, in the absence of epistasis, heritable differences between homozygous parents are determined by the additive effects of genes. Since the 1969 Stillwater test had reliable data from only three replications, a random process was used to select three replications/test from the tests which had four replications, thereby permitting a balanced design and analysis. An analysis of variance was conducted on the 120 plot means of the 10 parents, two years, two locations, and three replications/test. Results of the analysis may be found in Table 5. The significance of the locations mean square suggested that the total additive effects differed between Stillwater and Altus. This is *expressed* additive effects probably in relation to the severity of the disease at the respective locations rather than *inherent* differences, since the same parents were grown at both locations. Inspection of location means showed the disease to be more severe each year at Stillwater. Whether this was due to Stillwater's more northerly location, higher annual rainfall, or some other environmental variable is unknown. The total additive effects exhibited did not vary significantly from year to year, nor was the interaction between years and locations significant. The parents mean square was significant, implying that these parents did have genes with different additive effects for this trait. The first-order interactions revealed that relative performance among parents was constant from location to location but not from year to year. As exemplified by the nonsignificant second-order interaction, only a negligible portion of the interactions could not be associated with either years or locations.

The test for no genotype-environment interaction among the dominance components (2) was accomplished by a combined analysis of variance of the 120 V_r and 120 W_r adjusted estimates obtained from the 10 arrays, two years, two locations, and three replications/test in which the F_1 's were grown. The same replications were employed for this analysis as were used in the analysis of the additive components. Estimates of V_r and W_r were adjusted before analysis by dividing those estimates by the variance among parents within that replication. This adjustment minimizes the additive components in the test while increasing the prospects of detecting interactions of dominance effects with environment; it also tends to reduce the fluctuation of basic variability between

Table 5. Genotype by environment analysis of the additive components of variation.

Sources	df	Mean squares
Years	1	.9700
Locations	1	6.6200*
Years \times locations	1	3.3400
Reps within years and locations	8	.9238
Parents	9	21.6044**
Years \times parents	9	1.9444**
Locations \times parents	9	.6689
Years \times locations \times parents	9	.6333
Error	72	.4126

*, ** Significant at the 0.05 and 0.01 levels of probability, respectively.

environments which can mask between-environment comparisons in genetic systems (2). Results of this analysis are presented in Table 6. The years, locations, and years \times locations mean squares were not significant, which implies that rescaling was effective in reducing basic variability fluctuation between environments. Significance of the dominance mean square suggests that mean degree of dominance was either in the partial or overdominance range. Interactions of years \times dominance and locations \times dominance were not significant, whereas the second-order interaction was. Therefore, interactions with mean degree of dominance were present but could not be attributed to either locations or years. The significance of the arrays mean square indicated that the parents differed among themselves in the dominance effects of their genes. The significant years \times arrays interaction indicated that some parents' dominance effects changed relative to others from year to year; however, such changes could not be attributed to locations. A significant years \times locations \times arrays mean square pointed out that some relative dominance changes among parents could not be traced to either year or location effects. The lack of significance for the remaining four interactions provides additional evidence that epistasis was of negligible importance in the inheritance of wilt resistance in this material.

Parameter Estimates

Parameters may be estimated even though a trait has not completely fulfilled the assumptions of the analysis (11). However, estimates made under such circumstances are not as accurate as they would have been had all the assumptions been fulfilled.

Estimates were calculated in each replication; and standard errors of the mean, used in the tests of significance, were estimated by the variation of block values around the overall mean (19). Mean estimates and their significance levels are shown in Table 7.

Table 6. Genotype by environment analysis of the dominance components of variation.

Sources	df	Mean squares
Years	1	.0487
Locations	1	.0005
Years \times locations	1	1.1986
Reps within years and locations	8	.3587
Dominance	1	1.5974**
Years \times dominance	1	.0001
Locations \times dominance	1	.0024
Years \times locations \times dominance	1	.7889**
Arrays	9	.2103**
Years \times arrays	9	.0870*
Locations \times arrays	9	.0405
Years \times locations \times arrays	9	.0823*
Dominance \times arrays	9	.0214
Years \times dominance \times arrays	9	.0383
Locations \times dominance \times arrays	9	.0236
Years \times locations \times dominance \times arrays	9	.0153
Error	152	.0391

*, ** Significant at the 0.05 and 0.01 levels of probability, respectively.

Table 7. Mean parameter estimates and their levels of significance.

Param- eters	Altus			Stillwater		
	F_1 (1968)	F_1 (1969)	F_2 (1969)	F_1 (1968)	F_1 (1969)	F_2 (1969)
E_0	.72**	.29**	----	.37**	.18*	----
E_1	.55**	.34**	----	.44**	.21*	----
E_2	----	----	.49**	----	----	.44**
D	1.18*	1.92**	----	2.34*	2.00*	----
F	-.12	1.07*	1.07	1.42	.94	1.69
H_1	.69	.91*	1.47	1.68*	3.63*	4.68*
H_2	.97	.64*	1.14	1.30*	3.01*	4.09

*, ** Significantly different from zero at the 0.05 and 0.01 levels of probability, respectively.

E_0 , E_1 , and E_2 are estimates of parental, F_1 , and F_2 environmental variances, respectively. Estimates of E_0 were obtained from a between plot-within plot analysis of variance of the parental entries within each replication. Since the other parameters were estimated on a plot mean basis, the estimates of E_0 were converted to an equivalent basis by dividing the within plot mean square by the average number of plants/plot for the parental entries in that replication. E_1 and E_2 were calculated in an identical manner using F_1 and F_2 entries, respectively. The remaining parameters (D , F , H_1 , and H_2) are as defined by Jinks and Hayman (17) and were calculated using Hayman's (13) formulas. D is the additive genetic variance; F is an indicator of the relative frequency of dominant versus recessive alleles in the parents; and H_1 and H_2 are dominance genetic variances.

Since the estimates of environmental variation were all significantly different from zero, one must conclude that environment does influence the exhibition of wilt resistance. E_1 was larger than E_0 in three out of four cases while E_2 was larger than the corresponding estimates of E_0 and E_1 . D was significant in every instance and, with the exception of H_1 and H_2 in the 1969 Stillwater data, was larger than the other parameters in the same test. Therefore, additive genetic variance was present and was the most important source of variation in this material. F was inconsistent in sign; only one estimate out of six was significantly different from zero, and it was significant only at the 0.05 probability level. As a result, firm conclusions regarding the relative frequency of dominant and recessive alleles could not be reached. The majority of the H_1 and H_2 estimates were significantly different from zero; and in general, they ranked second to D in relative magnitude. Thus, we may reason that dominance variance was present in this material but that it was second in importance to the additive variance.

Several estimators were computed, using the parameters calculated for Table 7, to provide further information about the genetic behavior of wilt resistance. Each estimator was obtained in each replication, and standard errors of the mean were calculated as before. Means of those estimators and their 95% confidence limits are listed in Table 8.

Three estimates of degree of dominance are given in the table. All were between zero and one (i.e., in the partial dominance range) except for those obtained in the Stillwater 1969 F_1 which were greater than one (overdominance). None of the overdominance estimates included one (complete dominance) within its confidence interval. This fact coupled with that in the next paragraph has rather important breeding implications. If the trait exhibits overdominance for susceptibility in an occasional environment, this sporadic occurrence would tend to delay the eventual fixation of desirable homozygous recessive genotypes by selection since at those times the breeder would be inclined to select against the more heterozygous genotypes. He could thereby unintentionally nullify part of his previous selection progress. It also suggests that the breeder should not be so ruthless that he discards all lines except the very best ones, since to do so over a period of time would per-

Table 8. Mean estimators and their 95% confidence limits.

Estimators	F_1 (1968)	95% confidence limits	F_1 (1969)	95% confidence limits	F_2 (1969)	95% confidence limits
Altus						
Dominance 1*	.88	(-.54)-2.30	.51	.18-0.84	.17	(-.01)-0.35
Dominance 2*	.82	(-.02)-1.66	.70	.44-0.96	.36	(-.17)-0.87
Dominance 3*	.68	.15-1.21	.70	.48-0.92	.57	.36-0.78
$(\bar{F}_1 - \bar{P})\dagger$.27	(-.24)-0.78	.03	(-.11)-0.17	.06	(-.22)-0.34
$1/4 (H_2/H_1)$.26	(-.08)-0.60	.17	.12-0.22	.15	(-.02)-0.32
Heritability	.27	.12-0.42	.64	.36-0.92	.58	.29-0.87
Stillwater						
Dominance 1*	.85	.32-1.38	1.86	1.30-2.42	.67	(-.30)-1.64
Dominance 2*	.91	.64-1.18	1.36	1.16-1.56	.79	.15-1.43
Dominance 3*	.83	.43-1.23	1.56	1.42-1.70	.93	.30-1.56
$(\bar{F}_1 - \bar{P})\dagger$.11	(-.24)-0.46	.17	(-.66)-1.00	.12	(-.77)-1.01
$1/4 (H_2/H_1)$.21	.08-0.34	.21	.18-0.24	.21	.03-0.39
Heritability	.54	.10-0.98	.36	.17-0.55	.57	.02-1.12

* Dominance estimators one, two, and three in the F_1 were obtained using the formulas H_1/D , $(H_1/D)^2$, and $(V_{1L1}-E)/(W_{0L01}-E/n)$, respectively. These formulas in the F_2 were modified into $1/4 (H_1/D)$, $[1/4 (H_1/D)]^2$, and $(V_{2L2}-E)/(W_{0L02}-E/n)$, respectively. Interpretations of the symbols, V_{1L1} , V_{2L2} , W_{0L01} , W_{0L02} , and n , may be found in Jinks and Hayman's papers (11, 13, 16, 17). † Mean of the 45 F_1 (or F_2) versus midparent comparisons within each replication.

petuate homozygosity of intermediate genotypes in his materials.

The direction of dominance as indicated by $(\bar{F}_1 - \bar{P})$ revealed that the F_1 was more susceptible than its midparent value. However, the variation was such that in no set of data was this difference significantly different from zero. If this trend is real, it means that selection within early generation materials should often be effective in increasing the mean level of tolerance.

The ratio, $1/4 (H_2/H_1)$, estimates the average frequency of negative versus positive alleles in the parents (8). If the distribution is equal, the ratio should equal 0.25; if unequal, it should be smaller. Of the six estimates presented in the table, only one was very close to 0.25. Those remaining were 0.21 or less, and two of those were significantly different from 0.25. Apparently, the frequency of negative versus positive alleles in the parents was unequal. An examination of the means in Table 1 would suggest that the majority of genes in this population were for greater susceptibility.

Estimates of the number of effective factors, K , as defined by Mather (18) were highly erratic ranging from 112 to less than one. Only one estimate was significantly different from zero, and it was 0.13. As a result, reasonable doubt existed as to the validity of those estimates; and they were omitted from this paper.

Narrow-sense heritability estimates on a plot mean basis were calculated in the F_1 data using the formula derived by Crumpacker and Allard (8) and in the F_2 data using the modification given by Verhalen and Murray (22). All estimates were significantly different from zero. Four of the six estimates ranged from .54 to .64, which indicated that rapid selection progress would be possible in this material in most environments. This, of course, assumes that the techniques used in this experiment were utilized in those selections. The techniques considered most critical were spaced plantings, inoculation and late irrigation in the fall, use on a plant basis of the grading scheme devised herein (or a similar one), and selection on a row mean basis rather than on individual plants. It is noteworthy that the two lower heritabilities were obtained under circumstances peculiar to those individual tests. The estimate of .27 was obtained at Altus

in 1968 where plants/hill varied from one to four and where inoculations in the fall were not made (i.e., natural infection was depended upon to produce symptoms). The estimate of .36 was obtained at Stillwater in the 1969 F_1 where overdominance was present. The cause for the overdominance, presumably some environmental factor, cannot be determined; but it is well known that overdominance reduces narrow-sense heritabilities rather drastically when compared to similar models of no, partial, or complete dominance.

The quantitative genetic study reported within this paper was based on visual grades within a particular population. Other studies employing visual grades have been used to study disease resistance in cotton (9, 15, 23, 24 — to mention only a few). We wish to emphasize that the conclusions derived from such studies as to dominance versus recessiveness (9), degree of dominance (if present), number of genes (in some cases), heritabilities, etc., are conditioned to a large extent by the grading system used. Since grades are assigned subjectively, they will rarely be identical, even when the same individual assigns the same scale to the same population. Still, some sort of standardization of grades for each disease would clearly seem to be in order, so that results between different experiments could be compared more directly than is possible at the present time.

ACKNOWLEDGMENTS

We wish to gratefully acknowledge the correspondence and personal discussions with J. R. Barrow (New Mexico State University, University Park), W. D. Fisher and L. S. Stith (University of Arizona, Tucson), and S. Wilhelm (University of California, Berkeley) which have contributed materially to this paper. C. D. Ranney and C. F. Lewis (Cotton and Cordage Fibers Research Branch, Beltsville), and J. S. Kirby and R. E. Hunter (Oklahoma State University, Stillwater) read the manuscript, and their comments and criticisms also proved to be quite helpful.

LITERATURE CITED

- Allard, R. W. 1956. Estimation of prepotency from lima bean diallel cross data. *Agron. J.* 48:537-543.
- . 1956. The analysis of genetic-environmental interactions by means of diallel crosses. *Genetics* 41:305-318.
- Barrow, J. R. 1970. A genetic analysis of verticillium wilt tolerance in Acala cotton. *Proc. Beltwide Cotton Prod. Res. Conf.* p. 68. (Abstr.)
- Bell, A. A., and J. T. Presley. 1969. Temperature effects upon resistance and phytoalexin synthesis in cotton inoculated with *Verticillium albo-atrum*. *Phytopathology* 59:1141-1146.
- Brinkerhoff, L. A. 1949. Hypodermic injection as a method of inoculating cotton plants with *Verticillium albo-atrum*. *Phytopathology* 39:495. (Abstr.)
- Bugbee, W. M., and J. T. Presley. 1967. A rapid inoculation technique to evaluate the resistance of cotton to *Verticillium albo-atrum*. *Phytopathology* 57:1264.
- Cotton, J. R. 1965. Breeding cotton for tolerance to verticillium wilt. *USDA Bull. ARS* 34-80. 18 p.
- Crumacker, D. W., and R. W. Allard. 1962. A diallel cross analysis of heading date in wheat. *Hilgardia* 32:275-318.
- El-Zik, K. M., and L. S. Bird. 1970. Effectiveness of specific genes and gene combinations in conferring resistance to races of *Xanthomonas malvacearum* in upland cotton. *Phytopathology* 60:441-447.
- Fisher, W. D. 1968. Breeding cotton for tolerance to verticillium wilt. *Proc. Beltwide Cotton Prod. Res. Conf.* p. 230. (Abstr.)
- Hayman, B. I. 1954. The theory and analysis of diallel crosses. *Genetics* 39:789-809.
- . 1957. Interaction, heterosis, and diallel crosses. *Genetics* 42:336-355.
- . 1958. The theory and analysis of diallel crosses. II. *Genetics* 43:63-85.
- . 1963. Notes on diallel-cross theory. p. 571-578. In W. D. Hanson and H. F. Robinson (ed.), *Statistical genetics and plant breeding*. Nat. Acad. Sci.-Nat. Res. Council, Washington, D. C.
- Innes, N. L., and S. J. Brown. 1969. A quantitative study of the inheritance of resistance to bacterial blight in upland cotton. *J. Agric. Sci., Camb.* 73:15-23.
- Jinks, J. L. 1954. The analysis of continuous variation in a diallel cross of *Nicotiana rustica* varieties. *Genetics* 39:767-788.
- , and B. I. Hayman. 1953. The analysis of diallel crosses. *Maize Genet. Co-op. Newsletter* 27:48-54.
- Mather, K. 1949. *Biometrical genetics*. Dover Publications, Inc., London, 158 p.
- Nelder, J. A. 1953. Statistical models in biometrical genetics. *Heredity* 7:111-119.
- Presley, J. T., and L. S. Bird. 1968. Diseases and their control. pp. 347-366. In F. C. Elliot, M. Hoover, and W. K. Porter, Jr. (ed.), *Advances in production and utilization of quality cotton: Principles and practices*. The Iowa State Univ. Press, Ames.
- Stith, L. S. 1969. Another look at vert. *Proc. Beltwide Cotton Prod. Res. Conf.* pp. 33-35.
- Verhalen, L. M., and J. C. Murray. 1969. A diallel analysis of several fiber property traits in upland cotton (*Gossypium hirsutum* L.) II. *Crop Sci.* 9:311-315.
- Wilhelm S., J. E. Sagen, and H. Tietz. 1969. Dominance of sea island resistance to verticillium wilt in F_1 progenies of upland \times sea island cotton crosses. *Proc. Beltwide Cotton Prod. Res. Conf.* p. 31. (Abstr.)
- , ———, and ———. 1970. Seabrook (*Gossypium barbadense*) \times Rex (*Gossypium hirsutum*) crosses give verticillium wilt resistant, upland-type, all fertile offspring. *Proc. Beltwide Cotton Prod. Res. Conf.* p. 70-76.