Resistance to Verticillium Wilt in Cotton: Sources, Techniques of Identification, Inheritance Trends, and the Resistance Potential of Multiline Cultivars

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ABSTRACT

Greenhouse inoculation and field tests have identified sources of resistance to Verticillium wilt in *Gossypium barbadense* and *G. hirsutum* and to a lesser extent in *G. arboreum* and *G. herbaceum*. Reaction to wilt in *G. barbadense* ranges from near immunity against fungal vascular invasion to moderate susceptibility; and in *G. hirsutum*, from minimal resistance to high susceptibility. In resistance, F_1 plants of the cross [resistant *G. barbadense* × susceptible *G. hirsutum*] are always intermediate between the parents. Resistance is associated with the capacity of infected plants to recover and to escape infection of leaves. The potential of controlling Verticillium wilt of cotton by synthesis of genetically variable multiline cultivars derived from pedigreed wilt-resistant parents is presented.

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Additional key words: inoculation-box test, extra-long-staple cotton, Upland cotton, blending inheritance.

In California, Verticillium wilt of cotton, *Gossypium hirsutum* L., caused by *Verticillium albo-atrum* Rke. and Berth. (microsclerotial form), was first recognized in 1927 in the cultivar Acala in the Shafter-Wasco district of Kern County (6, 10). As the cotton acreage expanded northward in the San Joaquin Valley, the disease also spread. Inoculum may have been disseminated with seed (5), by wind, surface ground water (2), and contaminated equipment; or the disease may have appeared from indigenous inoculum developed on common weeds of the genera *Physalis*, *Solanum*, and *Xanthium*. Evans traced *Verticillium* infestations of cotton fields in New South Wales to weeds (4). In old agricultural areas, infestations on weeds may be further traceable to longstanding soil contamination that resulted from earlier cultivation of host crops such as potatoes. In the 1927 outbreak of wilt in cotton, Shapovalov and Rudolph (10) implicated potatoes as the source of infestation. Potato seed pieces commonly carry the fungus internally (3). Historically, the likelihood of widespread Verticillium wilt in parts of California is established by reports of unilateral branch dying in young, otherwise healthy, apricot trees in the San Joaquin Valley in the 1880's (1, 12), and of devastation of strawberries by brown blight early in this century in the Sacramento Valley (13, 18).

Today, major areas of cotton cultivation in California are infested with *Verticillium*. Infestations persist and resist nonhost rotations, particularly in heavy loam soils. Complicating the situation, and responsible, in our opinion, for the recent rapid spread of a particularly virulent defoliating form of the wilt organism (9) is the compulsory cultivation by legal decree of a single, pure cotton strain throughout the vast San Joaquin Valley, involving over 800,000 acres of cotton. In areas where climatic factors are favorable, the disease causes consistent yield reductions of one-third (14), and, in our experience, often of up to one-half, of the potential of this one variety. The lint quality is also reduced.

In 1965, we began to screen cottons from world sources for high resistance to Verticillium wilt, and to study the inheritance of resistance. Progress reports and a review of literature have been published (16, 19, 20). This paper summarizes several years of laboratory, greenhouse, and field studies on resistance, and points to avenues that have practical value for the solution of the cotton wilt problem in California.

MATERIALS AND METHODS.—*Greenhouse methods*.—Cottons evaluated for resistance in the greenhouse included accessions, F_1 hybrids, and progenies derived from single-plant selections of subsequent generations. Cotton seed received from out of state was rarely planted directly in the field, and the greenhouse, located outside the cotton-growing area, thus also served as a "quarantine station." Greenhouse tests consisted of inoculating uniform, vigorous cotton seedlings growing in narrow inoculation boxes with *Verticillium*, and rating the wilt reactions. The boxes were 15 cm wide at the top, tapering to 8 cm wide at the bottom, 44 cm high, and 82.5 cm long; the length was adapted to the width of the greenhouse benches. The sides were of 3-mm tempered Masonite, and the ends and bottom of redwood, 19 and 41 mm thick, respectively. The boxes

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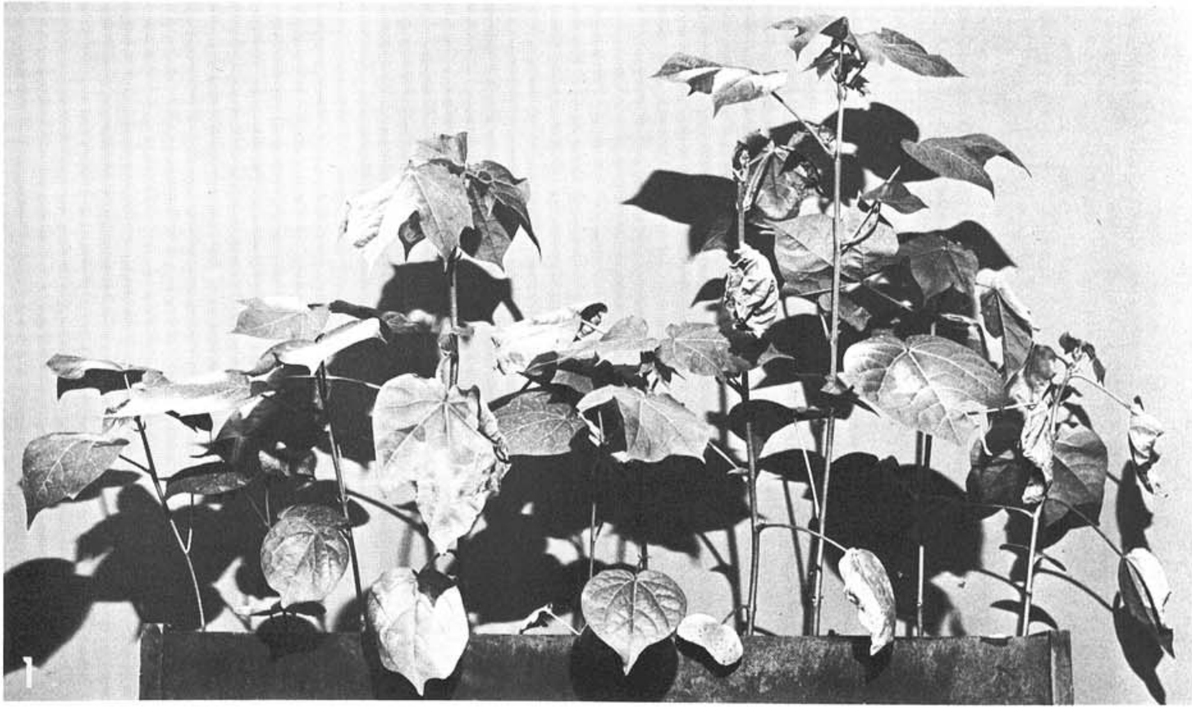
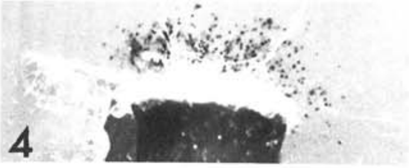
Fig. 1-5. Greenhouse inoculation-box technique and method of isolating *Verticillium*. **1)** Wilt-susceptible reaction of Acala cotton *Gossypium hirsutum*) 14 days after inoculation. **2)** Wilt-resistant reaction of Seabrook 12-B-2 (*G. barbadense*) 10 wk after inoculation. **3)** Petiole portions from 10 different plants cultured on 2% water agar containing bits of sterile barley straw; five are positive. **4)** Enlarged portion of cotton petiole and positive culture showing development of microsclerotia of *Verticillium*. **5)** Xerox-duplicated paper label selectively colonized by *Verticillium*. Microsclerotia facilitate identification.





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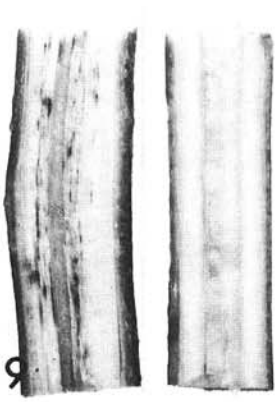
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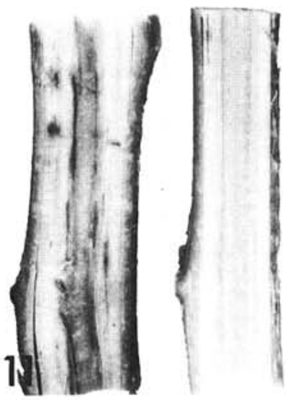
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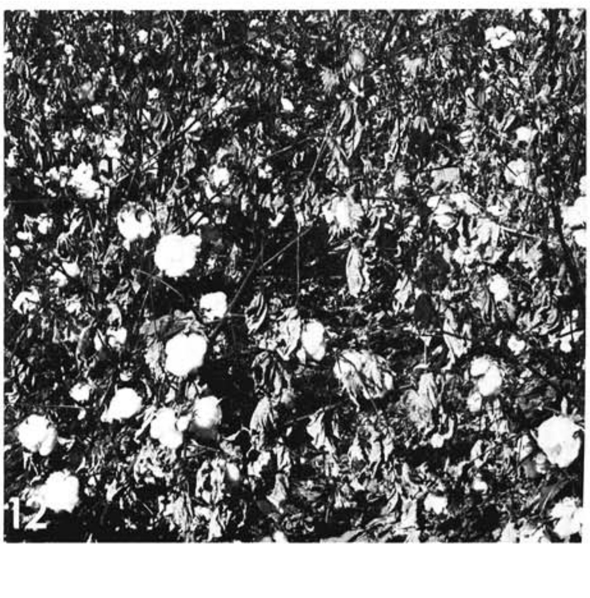
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were held together by steel strapping and kept slanted at a 20° angle by metal frames. The soil was fumigated with chloropicrin. Ten plants of a cotton strain were grown in each box from seed conditioned to germinate by immersion for one minute in water held at 80 C. After the roots were abundantly developed against the lower, tapered side of the box—plant height of approx. 30 cm—they were exposed by removing that side and inoculated with a suspension of *Verticillium* condidia. The inoculum was prepared from single-conidial transfer cultures of 20 different isolates obtained from severely defoliated Acala cotton. The isolates were maintained in the laboratory. After inoculation, the boxes were reassembled with new strapping. Vascular infection occurred immediately and symptoms appeared within 10-14 days (Fig. 1) when inoculations were made during periods of wide fluctuations in temp and light intensity.

The plants were scored for wilt symptoms at intervals of 2-3 wk, five times during the test. Scorings were made on a scale of 0-4; 0 indicated freedom from visual symptoms; 4, severe symptoms culminating in the death of the plant. Intermediate degrees of disease severity were indicated by scores of 1, 2, and 3. The scores were cumulated for each box and readily indicated relative wilt susceptibility. The scores did not adequately indicate the reaction of resistant plants which typically developed slight to moderate symptoms initially (scores 1-3) and subsequently recovered. Yet the consistent capacity to recover, as demonstrated in many inoculation-box tests, unquestionably identified resistance. For instance, wilt resistant cottons Seabrook 12-B-2 and Waukena White (*G. barbadense*) consistently showed seven to eight and three to four recovered plants, respectively, of the initial 10 (Fig. 2); whereas wilt-susceptible cottons, such as Acala (*G. hirsutum*), have never consistently yielded a single recovered plant. Thus, the inoculation-box test, provided a reliable, but merely preliminary, indication of the resistance level which was then further tested in the field. This technique, with slight modifications, has been used successfully for 8 yr.

Field tests.—Cottons surviving the greenhouse inoculation were grown to maturity in the boxes. They were selfed or used as parents in crosses. Seedlings of selfed-parent progenies and F_1 were grown individually in 8-cm diam peat pots for approx. 6 wk in the greenhouse and, after hardening in the lath house, transplanted to the field nursery in a highly wilt-infested area. The plants were spaced at approx. 50 cm in rows. The even spacing increased the reliability of evaluations for Verticillium wilt resistance. In F_1 populations of (*G. barbadense* × *G. hirsutum*) crosses, the disease evaluation was enhanced by abundant fruitfulness and phenotypical uniformity within crosses; however, F_2 populations showed a phenotypical variability within crosses that made accurate scoring for resistance to wilt impossible. Beginning approx. 6 wk after transplanting, and again at intervals of approx. 1 mo from there on until maturity, the plants were scored for symptoms of wilt, and a petiole of a selected leaf of each was cultured for *Verticillium*. Plants were scored from 0-4; 0 indicated the absence of visible symptoms; 4, a dead or nearly dead plant. The intermediate values of 2 and 3 indicated degrees of leaf yellowing, interveinal necrosis, defoliation, and terminal dieback. The score of 1 indicated slight or questionable symptoms such as incipient wilting or slight yellowing of leaves which may or may not be caused by *Verticillium*. The petioles, together with prenumbered and Xerox-duplicated labels, were surface-sterilized in a 0.1% solution of mercuric chloride for 3 min, rinsed in distilled water, and cultured in the laboratory on square plastic petri dishes containing 2% plain water agar and small bits of sterile barley straw (Fig. 3, 4, 5). Details of the technique have been published (21).

At harvest, the main stem of each plant was cut near the ground, and at a height of approx. 40 cm, and rated on a scale of 0-4 for intensity and pattern of vascular discoloration. The score of 0 indicated the absence of discoloration; 1, very slight streaking in the wood nearest the pith; 2, slight streaking distributed sporadically throughout the wood; 3, distinct dark discoloration throughout the wood; and 4, intense uniform discoloration and wood deterioration. The pattern of discoloration as seen in the stem cross section and the distribution of discoloration within the plant were considered to be a reflection of when, and how frequently, vascular infections occurred. These criteria also indicated whether the plant resisted systemic vascular invasion. For instance, discoloration only in the innermost wood indicated early-season infection followed by recovery; of the entire xylem, repeated vascular infection and xylem disintegration.

The wilt score of a plant, or the average wilt score of a homogenous cotton line (rounded off to the nearest half value) was based on the scores for symptoms and for vascular discoloration, and success of isolation of *Verticillium* from petioles. If vascular discoloration at 40 cm height was scored at 2 or higher, or if *Verticillium* was isolated from petioles during the growing season, or from discolored wood at the end of the season, the value of 1 was added to the highest symptom score. Wilt scores of 0-3 indicated resistance; 4-5, susceptibility. No cotton in our experiments has consistently scored 0. The score of 3 was

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Fig. 6-13. Field evaluation of Verticillium wilt resistance in cotton. **Fig. 6-8)** Cultivars Waukena White (*Gossypium barbadense*, wilt score 3) and Acala (*G. hirsutum*, wilt score 5). **6)** Early-season (June) wilt defoliation of Waukena White. **7)** Severe leaf symptoms and stunting in Acala. **8)** Recovery in Waukena White, which occurs by the first appearance of flower bracts (squares). **9)** Late-season vascular discoloration of main stem of Waukena White at ground line (left) and at 40 cm hight (right). **10-11)** Accession 584 of the Botanical Garden of Bonn, Germany (*G. barbadense*, wilt score 1). **10)** Early-season (June) symptoms typically appeared only in a single lower leaf which dehisced. Subsequent growth was free of symptoms. **11)** Vascular discoloration of main stem at ground line occurred primarily in the first wood formed (left) and was faint at 40 cm height (right). **12-13)** Field plots (1972) of experimental Upland cotton (*G. hirsutum*). **12)** Wilt-susceptible Acala SJ-1, showing wilt defoliation, terminal dieback, low boll set, and a yield of less than half of its potential. **13)** Wilt-resistant line selected from Oklahoma 141-5, showing an excellent mature crop with little loss of leaves from wilt. During boll development the plant becomes procumbent, but straightens again during maturity.

considered to represent the minimal resistance necessary to control the severe defoliating strain of *Verticillium*. This minimal field resistance is illustrated by our extra-long-staple experimental variety, Waukena White, which developed leaf symptoms of class 2 only early in the growing season (Fig. 6). In contrast to many Upland cottons, which showed severe stunting and leaf symptoms (Fig. 7), it developed no terminal dieback and quickly recovered from the early infection (Fig. 8); however, *Verticillium* was isolated readily from discolored vascular tissues of the main stem as late as harvest, 4 mo or more after the last evidence of leaf symptoms (Fig. 9) (23). Cottons with resistance scores 1.0-1.5 typically developed early-season symptoms in only one or two of the first-formed true leaves, which rapidly turned yellow and dehisced (Fig. 10). These symptoms may easily be mistaken as an effect of shading or ascribed to some other supposed cause, or they may be overlooked altogether. In this resistance class, the vascular discoloration at the time of harvest typically is of score 2 at the stem base; it is faint or absent at 40-60 cm height (Fig. 11). The *Verticillium* fungus remains viable in the discolored wood and is readily recovered in culture (21).

RESULTS.—The data (Table 1) are from arbitrary groups of five plants grown in the wilt nursery and were selected to illustrate the procedures upon which a field wilt score of a cotton line or F_1 was based. During the years 1965-1972, nearly 19,000 plants have been so scored; most were F_1. Regardless of their species affinity, the cottons were ultimately classed as wilt-resistant (scores of 1-3.5) or wilt-susceptible (scores of 4-5). Cottons that consistently failed to provide survivors from greenhouse inoculation-box tests were considered to be suceptible and usually not studied further.

Gossypium barbadense cottons consistently fell into resistance classes 1-3 in repeated field tests over 5 yr, and also were true-breeding for their specific resistance levels. A classification of these cottons, arranged in descending order of resistance levels follows. Berkeley accession numbers are given in parentheses, as our results represent wilt reactions only of lines derived from survivors of inoculation-box tests, and thus not necessarily of the original accessions. Highly resistant lines, with wilt scores of 1.0-1.5, were: Accession 584 of the Botanical Garden of Bonn, Germany (B123) (this cotton was labeled *G. arboreum*, but it is *G. barbadense*; its leaves are delicately

TABLE 1. Representative field wilt reactions of selected cotton lines illustrating the method used to arrive at a wilt score. Plants were scored separately for leaf symptoms and for vascular discoloration in the stems on a scale of 0-4. Positive laboratory isolation of *Verticillium* is indicated by figures in bold face. Wilt scores are based on visual symptoms, vascular discoloration, and laboratory isolation of *Verticillium*. Scores of 0-3 indicate resistance, 4-5, susceptibility

	Leaf symptoms					Stem vascular discoloration	
	Dates of symptom evaluation and culturing					at 40 cm	Wilt
Cotton line	June 9	July 1	July 20	Aug 9	Sept 3	Oct 15	score
Cotton line	June 9	July 1	July 20	Aug 9	Sept 3	Oct 15	score
Seabrook 12-B-2 [B106]	0	0	0	0	0	**1**	1
	0	0	0	0	0	1	0
	0	0	0	0	0	**1**	1
	0	0	0	0	0	**1**	1
	1	**0**	0	0	0	**2**	2
Shafter Sea Island [B104]	**2**	0	0	0	0	**2**	3
	1	0	0	0	0	**4**	2
	1	**2**	0	0	0	**3**	3
	1	0	0	0	0	**2**	2
	1	0	0	**0**	0	**2**	2
Waukena White [B55]	**2**	0	0	0	1	**2**	3
	2	0	0	0	1	**2**	3
	1	0	0	0	1	**3**	2
	2	0	0	0	0	**2**	3
	0	0	0	0	0	**2**	1
Gossypium hirsutum [B115]	0	**3**	**4**	**4**	D[a]		5
	2	**4**	**4**	D			5
	3	**4**	**4**	**4**	D		5
	3	**4**	**4**	**4**	D		5
	0	**3**	**3**	**3**	**3**		4
Rex [B4]	**2**	**2**	**3**	**2**	**2**	**4**	4
	0	**1**	2	**2**	**3**	**4**	4
	0	**0**	**2**	**2**	**4**	**4**	5
	1	**2**	**2**	**2**	**3**	**4**	4
	0	**2**	**2**	**2**	**4**	**4**	5

[a]D = plant dead.

fragrant of coumarin and it is our most wilt-resistant line); Seabrook 12-B-2 (B106); St. Kitt's Superfine (B79); Tanguis 28-85 (B103); Russian 5476-I (B211); and Russian CB3151 (B54). Moderately resistant lines with wilt scores of 2.0-2.5 were: Coastland (B56); Shafter Sea Island (B104); Ashmouni (B74); Domains Sakel (B71); and an Argentina line (B66). Lines with a wilt score of 3.0 or 3.5, indicating minimal resistance, were: Menoufi (B73), and Waukena White (B55). The selection from the Botanical Garden of Bonn often showed no external symptoms and only slight vascular discoloration at the stem base, from which Verticillium could be isolated.

Gossypium barbadense cottons which were classed as wilt-susceptible, but only on the basis of greenhouse inoculation-box tests, included strains of *G. barbadense* indigenous to British Honduras (B53), Guatemala (B57), Guadaloupe (B58), Colombia (B59), Brazil (B60, B172, B173, B174, B175), Montserrat (B61), Bolivia (B63), Argentina (B65, B67), Cuba (B49), Paraguay (B50), Guyana (B52), and Peru (B164). Old Pima (B75), P32 (B76), PS-1 (B77), and PS-2 (B78) were also susceptible.

Upland cottons (*G. hirsutum*) typically showed higher wilt susceptibility than extra-long-staple cottons of the species *G. barbadense*. Here the wilt scores ranged from 3-5, with the majority of cottons falling between 4.5 and 5. A long list of wilt-susceptible Upland cottons, including recent and old varieties cultivated in the United States and varieties from Syria, Pakistan, East Africa, Russia, and Australia, has been presented in a previous report (19). Botanical gardens have been an excellent source of old varieties, and of uniform old lines labeled only *G. hirsutum*. All of these were found to be susceptible to wilt. In no foreign Upland cotton, nor in old American *G. hirsutum* varieties received under names such as Mebane, Triumph, Express, Meade, Misdel, have we found wilt resistance equivalent to that of present-day New Mexico lines B1149, 8116, 9210, 8829, 3080, or of Hopi Acala 6-1-5 and Alabama H257. Wilt scores of these ranged from 3.5-4.5. The Uganda variety 181, reported as wilt-resistant by Kamal and Wood (7), proved susceptible, as did also the old Russian standard varieties 36M2, 108F, 152F, 9123-I, K-K351, K-K1086, and OSH-11.

In selections from three different Upland cottons, wilt scores of 3-3.5 were consistently obtained during the past 3 yr. These represent the highest levels of resistance we have secured thus far in Upland cottons. In our tests, Acala SJ-1 fell far short of the resistance present in these lines and has served as a wilt-susceptible check (Fig. 12). Original lines providing the resistance were: Paymaster 266-69 composite, Oklahoma 141-5, and Deltapine 5836. Paymaster 266-69 composite was developed by D. C. Hess from the cross [F_1 (Arizona 6024-11-1-2-C × DPL5540) × F_1 (P-101A-B4 × P-105-B4)]. The parents P101A-B4 and P105-B4 were Paymaster lines of the Acco Seed Co., Plainview, Texas (D. C. Hess, *personal communication*). Oklahoma 141-5 (Fig. 13) was a selection from New Mexico 8060-3 made in Oklahoma (L. M. Verhalen, *personal communication*). Our several derivative lines (17) have resulted from single-plant selections, first from survivors of greenhouse inoculation-box tests, and then from progeny rows in the wilt nursery.

Of 51 Asiatic stocks of *G. arboreum* and *G. herbaceum* obtained from the Regional Collection of the Delta Branch Experiment Station, Stoneville, Mississippi, nine survived greenhouse inoculations and, in tests conducted in the field only in 1968, were highly resistant. They were *G. herbaceum* CB2590, and *G. arboreum* A2-12, A2-15, CB2522, Texas 2112, 2113, CB2660, CB2700, and CB2546. Pambe Boumi, an Iranian cotton developed from *G. herbaceum*, also showed excellent wilt resistance in the field.

Small numbers planted of the species *G. tomentosum* Nutt. syn. *G. sandvicense* Parl. and *G. trilobum* Fryxell were found to be extremely and moderately wilt-susceptible, respectively.

Wilt reactions of F_1 (*G. barbadense* × *G. hirsutum*).—Several years ago, we attempted to transfer resistance of *G. barbadense* to the Upland phenotype. Our data (Table 2) show field wilt reactions of F_1 of 245 different crosses, summarize those presented in an earlier report (22), and confirm previous studies (15). The crosses were grouped into 10 classes according to ratios of resistance and susceptibility contributed by the parents. In crosses between wilt-susceptible cultivars of *G. hirsutum* and resistant cultivars or wild types of *G. barbadense*, F_1 were intermediate in morphology, flower color, and resistance to wilt, typical of the "blending" inheritance discussed by Stephens (11). They also showed striking heterosis and were fruitful. The level of resistance to wilt in F_1 approached, but was always less than, that of the resistant parent. Thus, wilt resistance derived from *G. barbadense* was dominant over wilt susceptibility. Backcrossing of wilt-resistant F_1, F_2, or F_3 to wilt-susceptible Upland cottons (class IV) yielded susceptible and resistant individuals in a ratio of approx. 1:1; backcrosses to the wilt-resistant parent (class V) gave all-resistant offspring. The few F_1 individuals classed as wilt-susceptible in certain crosses (see classes I, II, VI, IX, X, XI) may emphasize the difficulty (well known to us) of always clearly distinguishing between the intermediate scores of 3.5, minimal resistance, and 4, moderate susceptibility. The wilt reactions of all of the resistant Upland cultivars studied to date and of many of the *G. barbadense* × *G. hirsutum* F_1 hybrids lay in this range. The wilt resistance of classes 1-3 is clear-cut, as is also wilt susceptibility of class 5. Crosses between resistant nonhomozygous hybrids (class XIII) yielded predominantly resistant offspring.

Concept of wilt-resistant multiline cultivars.—Stephens stressed that maximum usefulness of a cotton cultivar; i.e., long varietal life, stability of production, and broad adaptation to environments, depends upon inherent genetic variability in contrast to genetic homogeneity (11). The short usefulness of Acala SJ-1 in California on 800,000 or more acres and its inadequate performance from the start in wilt areas point to the need for genetic diversification in cotton cultivars. This may be achieved either by mixing seed of pure lines, or by utilizing the inherent genetic variability, which the dominant nature of wilt resistance derived from *G. barbadense* makes possible. The results obtained to date make us favor the latter.

Crosses of class VIII (Table 2), in which both parents were wilt-resistant hybrids derived from recent *G. barbadense* × *G. hirsutum* crosses gave predominantly resistant offspring (22). Thus, the possibility exists that

TABLE 2. Frequency array of field wilt scores among F_1 plants of 10 classes of crosses involving *Gossypium hirsutum* (susceptible) and *G. barbadense* (resistant). Scores of 0-3.5 indicate resistance, and scores of 4-5, susceptibility

Class of cross	Description and field wilt scores of parents	Number of crosses	Number of plants: Resistant (R) [0-3.5]	Number of plants: Susceptible (r) [4-5]
I	r × R Acala (4.0-4.5) × *G. barbadense*	18	211	1
	non-Acala (4.5-5.0) × *G. barbadense*	4	54	22[a]
	R × r *G. barbadense* (1.5-3.0) × Acala (4.0-4.5)	20	276	6
VI	$F_{1,2,3}$ (R × R) × r *G. barbadense* × Upland cottons[b]	27	280	17[c]
II, X	R × R *G. barbadense* (1.0-3.0) × *G. barbadense* (1.0-3.0) or (R × R) × (R × R)	16	149	2
IV	$F_{1,2,3}$ (r × R) × r Backcross to Upland cottons	22	132	115
V	$F_{1,3}$ (r × R) × R Backcross to *G. barbadense*	25	286	0
IX	$F_{1,2,3}$ (r × R) × $F_{1,2,3}$ (R × R) Backcross to *G. barbadense*	51	503	3
VIII	$F_{1,2,3}$ (r × R) × $F_{1,2,3}$ (r × R)	36	310	38
XI	$F_{1,3}$ [(r × R) × r] × R	6	84	4
XIII	$F_{1,2,3}$ [(R × R) × r] × $F_{1,2,3}$ (r × R)	20	231	25

[a]19 of these were from one cross.
[b]Included Acala and non-Acala cultivars.
[c]Susceptible individuals appeared in four of the crosses.

parental combinations could be found which would combine in a variable offspring the qualities of wilt resistance, high yield, early maturity, and excellent fiber properties, leading to genetically variable multiline cultivars of long usefulness. Experiments are in progress to test the hypothesis.

DISCUSSION.—Good correlation has been achieved between greenhouse inoculation-box tests and field evaluations of cotton varieties, species, and hybrids for resistance to Verticillium wilt. Many cotton lines, particularly resistant lines used as parents, were tested annually for several years. All cotton lines and species studied to date became infected by *Verticillium* after greenhouse inoculations as well as planting in the field wilt nursery. All showed a degree of vascular discoloration, and *Verticillium* was isolated from plants regardless of whether or not they developed foliage symptoms. Thus, no cotton line received the wilt rating 0, indicating immunity to vascular invasion, but individuals approaching this immunity have been selected. Significance was attached to the capacities of infected plants to recover or resist symptom expression. These capacities are associated with the exclusion of systemic infection from leaves and many be related to anatomical features of the wood or to the production of host-induced antifungal toxins.

Gossypium barbadense contains many sources of high resistance; *G. hirsutum* cultivars contain none. Three Upland cottons, namely derivatives of Paymaster 266-69, Oklahoma 141-5, and Deltapine 5836, were minimally resistant. The appearance of resistance in the Upland cottons may reflect past introgression of *G. barbadense* characters into Upland varieties cultivated during colonial times. Its appearance is no more surprising than the occasional surfacing of the dominant okra-leaf character in uniform varieties having "normal" leaves. Conceivably, the variety Seabrook, selected for resistance to Fusarium wilt around 1890-92 by E. L. Rivers of James Island, South Carolina (8, 21) and grown rather widely for a time in the southeastern United States, contributed the introgression.

In crosses involving wilt-resistant *G. barbadense* and wilt-susceptible *G. hirsutum*, F_1 plants are resistant. The level of resistance is intermediate between the resistance levels of the parents. Thus, in certain crosses where the resistance level of both parents is low (class 3), wilt-susceptible individuals may appear in the F_1. The basic inheritance trend, however, remains the same.

The dominant inheritance of resistance makes it possible to produce wilt-resistant multiline cultivars of cotton; they may be either synthesized by crossing pedigreed, resistant parents or derived from selected F_1 individuals maintained as clones. The multiline cultivar conserves both variability and heterosis, and would also be expected to deter the rapid increase of disease in the presence of newly introduced *Verticillium* strains.

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