Gossypium hirsutum subsp. mexicanum var. nervosum, Leningrad Strain— A Source of Resistance to Verticillium Wilt

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ABSTRACT

Reports by investigators in the USSR that *Gossypium hirsutum* L. subsp. *mexicanum* var. *nervosum*, a wild, deep-rooting, perennial, short-day, cold-tolerant, Mexican species, is resistant to Verticillium wilt have been confirmed by greenhouse studies and field experimentation in the San Joaquin Valley of California. In both vegetative and fruiting phases of growth, the resistance effected localization of *Verticillium* to xylem tissues of the lower stem and prevented dehiscence of infected leaves and other symptoms. Resistance was transferred to hybrids with Upland cottons. The F_1, though developing rather extensive systemic vascular and leaf infection, was rated resistant. Likewise, corroborating reports from the USSR, the F_2 segregated for resistance and susceptibility in a ratio of approximately 3:1, which suggests dominant monofactorial inheritance. The botanical status of the wild Mexican cotton is clarified.

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Resistance to Verticillium wilt of cotton, caused by *Verticillium albo-atrum* Rke. and Berth. (microsclerotial form), has been found in wild and cultivated cultivars of *Gossypium barbadense* L., namely in accession 584 of the Botanical Garden of Bonn, Germany, in the cultivars Seabrook 12-B-2, St. Kitts, Tanguis, Coastland, Menoufi, and Waukena White, and in certain Russian extra-long-staple varieties. Resistance decreases in the

order given, from the near freedom of apparent vascular infection and leaf symptoms seen in accession 584 from Bonn, to the systemic infection and development of early-season symptoms followed by recovery in Waukena White (31, 32, 33, 39). Attempts to transfer the resistance by interspecific hybridization to the susceptible Upland cottons, *G. hirsutum* L., have had only limited success (5, 34). It is well-known, and is also our experience, that hybrid progenies of such crosses, particularly where Acala cottons are involved, tend to show less resistance the more Upland varietal characteristics they have. Thus, backcrossing, unless it is to the resistant *G. barbadense* parent, generally leads to loss of resistance.

In addition to the genetic problems encountered in transferring wilt resistance of *G. barbadense* to *G. hirsutum*, economic controls in the USA limit the use of *G. barbadense* in varietal improvement. *Gossypium barbadense* and its hybrids may be grown commercially only under provision of highly restricted acreage allotment for extra-long-staple cotton (U.S. Fed. Agric. Adj. Act, Sec. 347a, 1938). In the San Joaquin Valley of California the law (Statutes of Calif., Chap. 299, 1925) eliminates commercial cultivation of *G. barbadense* altogether and demands that the variety grown exclusively be Acala cotton (*G. hirsutum*) originating from the common seed stocks developed under the one-variety breeding program of the USDA Cotton Research Station, Shafter, Calif. The area thus legally forced into varietal "monoculture" of Acala cotton currently comprises 800,000 to 1 million acres. Unhappily for many growers, 15-20% of this land is infested by highly pathogenic strains of *Verticillium*, and the present single legal variety, Acala SJ-1, is extremely susceptible to a number of these strains; its predecessor, Acala 4-42, is also susceptible. In 1966, a strain of *Verticillium* considered to be new to the San Joaquin Valley and to possess higher virulence to Acala cotton than strains previously known was identified (23). Since then, disease losses have soared, and cotton growers in the wilt-infested areas of the eastern and central San Joaquin Valley, still bound to plant only the one wilt-susceptible cotton, have suffered severe economic hardship. As noticed by Ranney (18), cotton cultivation has shifted from the afflicted regions to newly irrigated land in western parts of the Valley.

In view of these difficulties, a source of resistance other than *G. barbadense*, preferably *G. hirsutum*, would seem to be prerequisite to the solution of the wilt problem of the cotton industry of the San Joaquin Valley through breeding, but, except for investigations by scientists of the USSR, wild *G. hirsutum* has not been systematically explored for resistance.

At the First International Congress of Plant Pathology held in London in 1968, N. N. Guseva, of the Institute of Plant Protection, Leningrad, presented evidence that *G. mexicanum* Tod., syn. *G. hirsutum* f. *mexicanum* or *G. hirsutum* L. subsp. *mexicanum* (Tod.) Mauer var. *nervosum* (Watt) Mauer, called herein the "wild Mexican cotton", was resistant to Verticillium wilt. Resistance prevented symptom development and was correlated with levels of caffeic acid detectable in seedlings. The original Mexican stocks were collected during the 1930's by N. Vavilov (D. V. Ter-Avanesian, *personal communication*). Subsequent selection in the USSR, during which Yucatan and Chiapas strains of wild *G. hirsutum* were found to be susceptible to wilt, produced the resistant wild Mexican cotton reported herein (1).

In experiments in the USSR, the wild Mexican cotton used as a root stock protected the wilt-susceptible Upland scion variety 1306-DV from infection, and conversely, as a scion grafted onto the variety 1306-DV, the wild Mexican cotton became only slightly infected. In crosses of the wild Mexican cotton with the wilt-susceptible Upland varieties 1306-DV and S4727, the F_1 was resistant, but culturing of stem vascular tissues revealed the presence of the fungus (22). Resistance was also found in F_2 and F_3 populations, in ratios suggesting monohybrid inheritance of dominant factors (12, 13, 15). Backcrossing of wilt-resistant F_3 to the original wilt-susceptible Upland parents gave resistant individuals, some with qualities of earliness, high yields, large bolls, favorable lint percentage, and long, strong fiber (3, 14, 17); this appears to be evidence of an independence of assortment greater than that observed in progenies of crosses between *G. hirsutum* and *G. barbadense*. Ter-Avanesian, in 1969, reported that the wild Mexican cotton was also resistant to Fusarium wilt (24, 25). Abilkhanov and Samoilov, on the other hand, noted the same year that the wild Mexican cotton had collapsed from Verticillium wilt in Uzbekistan (2).

In 1969, selections from backcrosses of F_3 (C-4727 × wild Mexican) to wilt-susceptible, early-maturing Uplands, planted on 260 ha. of wilt-infested land in Tashkent, remained free from wilt symptoms until harvest, except for 3-5% which had succumbed earlier. Yields were at least twice those of the old standard varieties 108 F and 153 F, which showed 80-90% mortality from wilt. The following year, more than 8,000 ha. were planted experimentally to wilt-resistant selections, and in 1971 the varieties Tashkent 1, 2, and 3, with wilt resistance derived from the wild Mexican cotton, were released, and planted on 200,000 ha. In 1972, over 1 million ha. were planted. Yields in the vicinity of 4,640, 4,520, and 4,490 kg/ha. of seed cotton—equivalent to approx. 2.5 500-pound bales of lint per acre—were reported for the varieties Tashkent 1, 2, and 3, respectively (16, 42, and D. V. Ter-Avanesian, *personal communication*).

Scientists in the USSR thus were among the first to extensively collect and systematically study the wild cottons of Mexico. In 1933, Harland predicted that the cotton-growing industry would undoubtedly reap a rich reward from their researches (6); that prediction seems to have come true.

The present study builds on our previous work (35, 36, 37) and has two objectives: to clarify the botanical status of the wild Mexican cotton, and to determine whether it and its hybrids with wilt-susceptible Upland cottons are resistant in the San Joaquin Valley of California. We provide partial answers.

MATERIALS AND METHODS.—*Identity of the wild Mexican cotton.*—Agostino Todaro, director of the Royal Botanic Garden at Palermo, described *G. mexicanum* briefly in 1868 (26), and in 1878 gave a full description with an excellent color plate (27). The shrubby plant, of no agronomic value, was described as

many-branched, perennial, and winter-hardy, having broad, glabrate, predominantly three-lobed, prominently veined leaves, and small, pale-yellow flowers with rose-purple petal spots. The bolls were 3- or 4-locked and blunt, with short, reddish-brown fiber and fuzz (Figs. 1-4). Todaro received the Mexican seed in 1864 from Joseph Decaisne, director of the Jardin des Plantes, Paris, labeled "Coton sauvage de Siam dit Siam clair arborescente et vivace" which we translate as "wild cotton of Siam, called light-colored Siam, arborescent and perennial." Inasmuch as Todaro's description of the cotton refers to a "reddish" fiber, "light-colored" must refer to flower color. Todaro's illustration, however, clearly shows white fiber. This contradiction is explained by segregation of seedlings for fiber color. Certainly the cotton did not originate in Siam (9); we believe that it was probably Boursier de la Riviere, a French consular agent who resided in California during the 1850's and traveled extensively in Mexico collecting seed and herbarium specimens for Joseph Decaisne, who first brought the wild Mexican cotton to Europe (4).

Watt in India, influenced by early papers of Willis (40) and Wight (30) on cultivation of Mexican cotton (albeit New Orleans seed), in 1907 applied the name *G. mexicanum* to glabrate Upland cottons of Mexican origin known only in culture in America, Africa, and India; he restricted the name *G. hirsutum* to hirsute cultivars (28). As shown by Lewton (9), the Watt scheme was formulated in disregard of Todaro's careful description and illustration of *G. mexicanum* and was therefore taxonomically unsound. Lewton also identified the exact counterpart of Todaro's illustration of *G. mexicanum* among wild cottons collected by Palmer in Mexico near Victoria (Tamaulipas) in 1910; he concluded that it was never a cultivated form and could have had no part in the development of the American Upland cultivars. Johnson (8) nonetheless persisted in the view that many Upland varieties originated from *G. mexicanum*. Subsequently, Watt erected the species *G. nervosum* from herbarium specimens of a densely branched cotton shrub, prepared by Palmer in 1910 while collecting in the Mexican state of Veracruz, and preserved at Kew. Five prominent veins ending at the lobe apices and curved in such a way as to appear arched, characterized the leaves (29).

Mauer (10) summarized the vast information on wild cotton which he gleaned from reports on an expedition of S. M. Bukasov to Mexico and Central America in 1925 and 1926, sponsored by the Institute of Applied Biology, Leningrad. He called attention to the great diversity of morphological types of wild cottons assignable to *G. hirsutum*, namely: annual forms similar to the cultivars Acala, Triumph, and Durango; perennial, shrubby, short-day forms unlike any cultivars; and arborescent types long known as Bourbon and Marie-Galante cottons. Grown at Tashkent, the wild Mexican cottons were shown to hybridize with cultivated forms of *G. hirsutum*, and to produce fertile offspring. Zaitsev identified one shrubby accession as *G. mexicanum* Tod. (41).

In 1937, Roberty, also recognizing that *G. hirsutum* embraced perennial wild and annual cultivated forms, reduced *G. mexicanum* Tod. to *G. hirsutum* forma *mexicanum*, and a few years later to *G. hirsutum* var. *mexicanum* (19, 20). In 1950, Roberty reduced *G. nervosum* Watt to *G. hirsutum* subsp. *latifolium* (Murr.) var. *nervosum* (Watt) Rob. (21).

Hutchinson (7), in 1951, on the basis of morphological differentiation and geographical distribution, grouped the enormous intraspecific variability of *G. hirsutum* into seven races. He did not force his taxonomy into the existing maze, or indicate whether synonymy might occur between any previously described taxa.

Mauer (11), convinced that *G. nervosum* Watt and *G. mexicanum* Tod. designated essentially identical intraspecific taxa within wild, perennial *G. hirsutum*, reduced them to *G. hirsutum* subsp. *mexicanum* (Tod.) Mauer var. *nervosum* (Watt) Mauer. We received a few seed of this cotton, for convenience labeled only *G. mexicanum* var. *nervosum*, from D. V. Ter-Avanesian, director of the Library, USSR Academy of Sciences, Leningrad, in the fall of 1969, through the courtesy of Paul Fryxell.

Evaluation of resistance.—In the spring of 1970 we conducted a greenhouse test for resistance using the method described previously (38). After inoculation with *Verticillium*, the wild Mexican cotton became infected promptly, and severe symptoms developed quickly. Only two of the 10 inoculated plants recovered. Because of the few seed then available, we could not run more extensive greenhouse tests. However, we attached significance to the evident capacity to recover, comparable to that of Waukena White, our experimental extra-long-staple variety (39); Waukena White typically shows recovery in 20-30% of greenhouse-inoculated plants.

Field tests.—Direct-seeded in a short progeny row in 1970 in a heavily wilt-infested nursery, the wild Mexican cotton grew vigorously and did not develop symptoms of wilt. Waukena White and Acala SJ-1 were planted as checks; the former developed slight leaf symptoms only in the spring, the latter severe leaf and dieback symptoms in spring and late summer. The weather that year was favorable for wilt; the disease occurs most severely when soil and air temp during a portion of each day for two or more weeks are below 27 C (Fig. 5).

In October, 1970, two plants each of Acala SJ-1, Waukena White, and the wild Mexican cotton, were dug from the field for serial culturing of xylem tissues for *Verticillium*. The branches were numbered in sequence (Fig. 6). Of each branch, ten petioles and one sample each of base, middle, and tip sections were cultured, as well as samples from selected levels throughout the main stem and the root. In Acala SJ-1 all cultures from root to stem and branch apices were positive (Fig. 7); petioles were not cultured because the severity of symptoms excluded any doubt about infection. In contrast, Waukena White (Fig. 8) and the wild Mexican cotton (Fig. 9) yielded only occasional positive cultures from the base of the main stem and/or lateral branches. The leaves were entirely without symptoms. Of a total of 272 petioles cultured from the two wild Mexican plants, only two yielded *Verticillium*. Vascular discoloration (Fig. 10) was severe throughout the xylem cylinder in Acala SJ-1, and limited to the center of the cylinder in Waukena White; in the wild Mexican cotton, it was slight, and only a few central vessels were affected.

In 1972, wild Mexican cotton seedlings grown from our

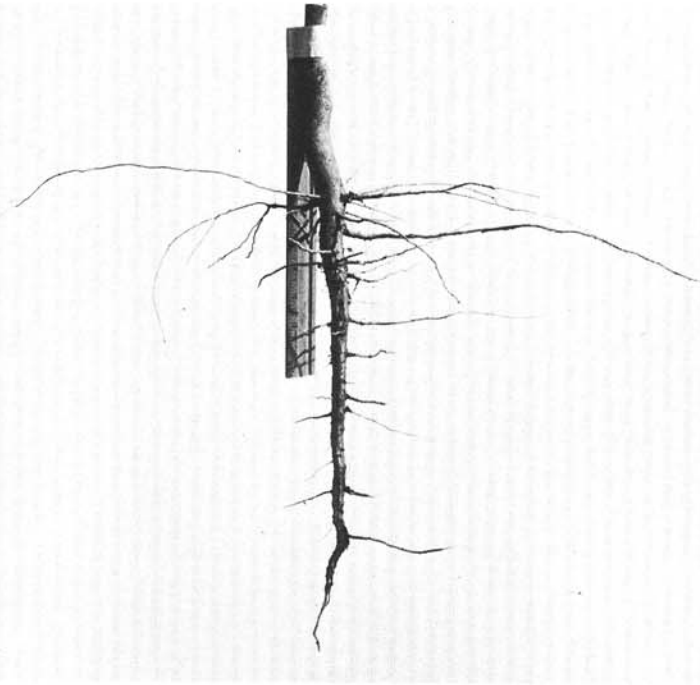


Fig. 1-4. Morphology of *Gossypium hirsutum* subsp. *mexicanum* var. *nervosum*, growing in the wilt nursey. **1)** Growth habit of nearly mature plant, Aug. 20, 1970; height 150 cm. **2)** Detail of leaf, square and flower, Oct. 15, 1970. **3)** Mature bolls, Nov. 11, 1971. **4)** Root habit. Ruler is 30 cm long.

own seed were transplanted to a progeny row in the wilt nursery. As in the 1970 test, the plants grew vigorously and without obvious symptoms of wilt. In late August, 1972, when the commercial Acala SJ-1 was developing severe symptoms of wilt, again the petioles and branches of two *G. mexicanum* plants were cultured serially for *Verticillium*; of 208 and 254 petioles, 14.8 and 3.5%, respectively, were positive. The infected leaves were symptomless. Thus, in its reaction to wilt in the field, the wild Mexican cotton appeared to have the type of resistance that we reported previously (39) for the extra-long-staple cotton Waukena White, namely a capacity to recover from infection. In the case of Waukena White, we attributed recovery to a capacity to localize infection in the xylem tissue and to prevent it from spreading to the leaves. The wild Mexican cotton appears to be less able to localize infection than Waukena White, but to have the capacity to resist symptom development in the infected leaf. This resistance would not seem to be effected by host-induced polyphenols, because the *Verticillium* fungus remains alive. We have suggested earlier that cotton leaves develop symptoms only after they themselves become infected, and we have used the criterion of leaf infection in scoring plants for resistance (31, 34, 38).

Resistance of the wild Mexican cotton during fruiting.—To test the hypothesis that the wild Mexican cotton may only appear to be resistant to wilt because, as a short-day plant, it fails to fruit during its first growing year in our latitude, cuttings were taken from the field during flowering and rooted in the greenhouse in November 1971. The following year, 24 cuttings were set in the wilt nursery together with seedlings grown and transplanted that spring. The cuttings grew vigorously in the field and, in contrast to the seedlings, flowered and fruited during the entire 1972 season. But, like the seedlings, the cuttings developed no symptoms of wilt, and detailed serial culturing of roots, stems, branches, and leaves late in the season revealed an extent of vascular infection comparable to that of plants grown from seed, which did not fruit.

Wilt reaction of hybrids.—The wild Mexican cotton hybridizes readily with Upland cottons. In 1972 eight and six F_1 individuals of wild Mexican × Upland crosses BX833 and BX837, respectively, were transplanted as seedlings to the wilt nursery. The Upland parents were our lines derived from *G. hirsutum* × *G. barbadense* ancestry, and were moderately resistant to wilt. Both F_1 progenies remained free of wilt symptoms during the entire year. Phenotypically and in photoperiodic response, the plants were intermediate between the parents and matured cotton in late fall. Cultures of stem tissues also revealed a more extensive vascular infection than that which occurred in the wild Mexican cotton check. Of 93 and 128 leaves cultured from two F_1 plants of cross BX837, 22 and 60%, respectively, developed positive cultures; of 125 and 194 leaves of two plants of cross BX833, 14 and 3%, respectively, were infected. Eight cuttings each, taken in October 1971 from a single F_1 plant of each cross, and transplanted to the wilt nursery in 1972, flowered and fruited abundantly and, although vascular discoloration and infection as determined by culturing of stems, branches, and leaves (Fig. 11) was more extensive than in the wild Mexican parent, they were resistant. Infection was not expressed as typical wilt symptoms in leaves, and within each of the two clones, reactions of all plants were identical as to pattern of vascular infection, vascular discoloration, and resistance to symptom development. This study of identical clonal replications, in which no individual escaped wilt, provided reliable evidence both for the resistance of the wild Mexican cotton and for the heavy, uniform infestation of the field soil with *Verticillium*.

Also in 1972, 46 and 25 F_2 individuals of crosses BX833 and BX837, respectively, were transplanted to the wilt nursery as seedlings. A group from each cross had been

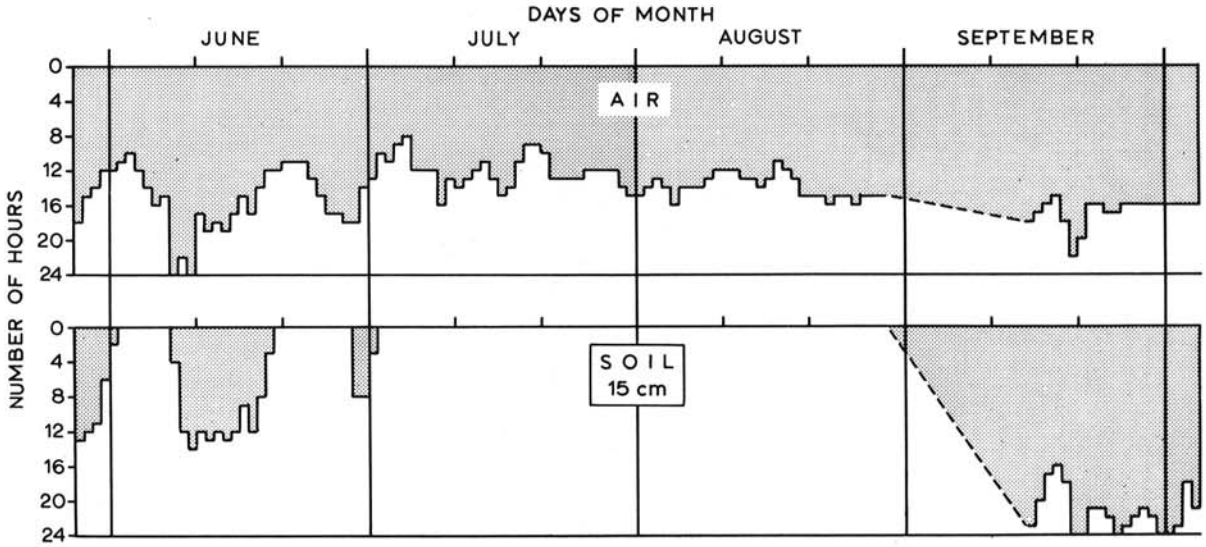
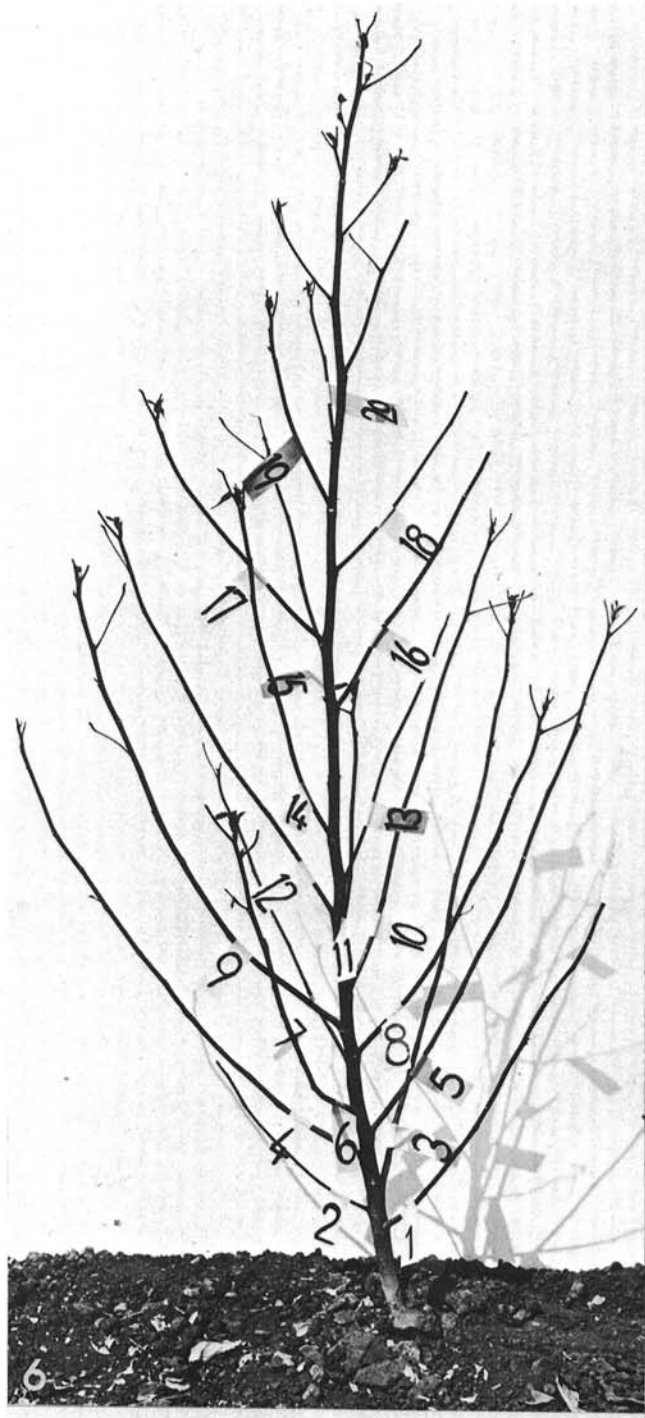


Fig. 5. Air and soil temp at the wilt nursery in 1970, plotted to show the number of hours per day below 27 C.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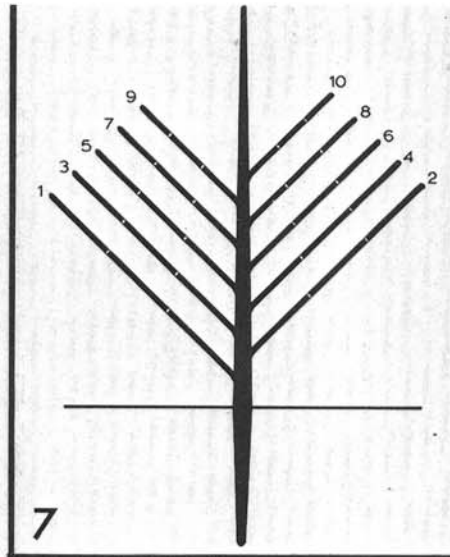
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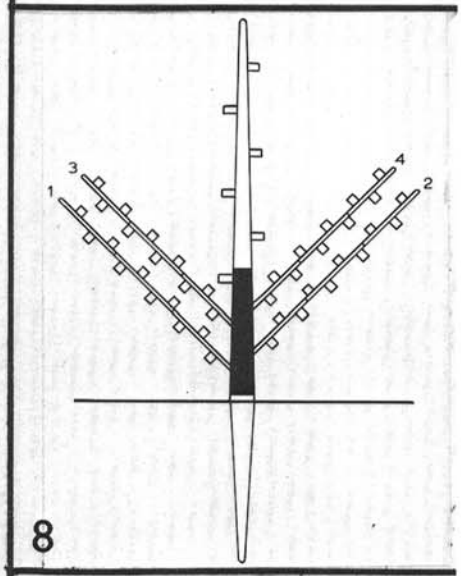
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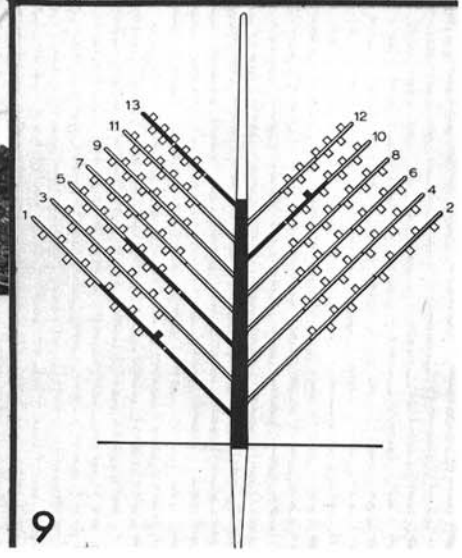
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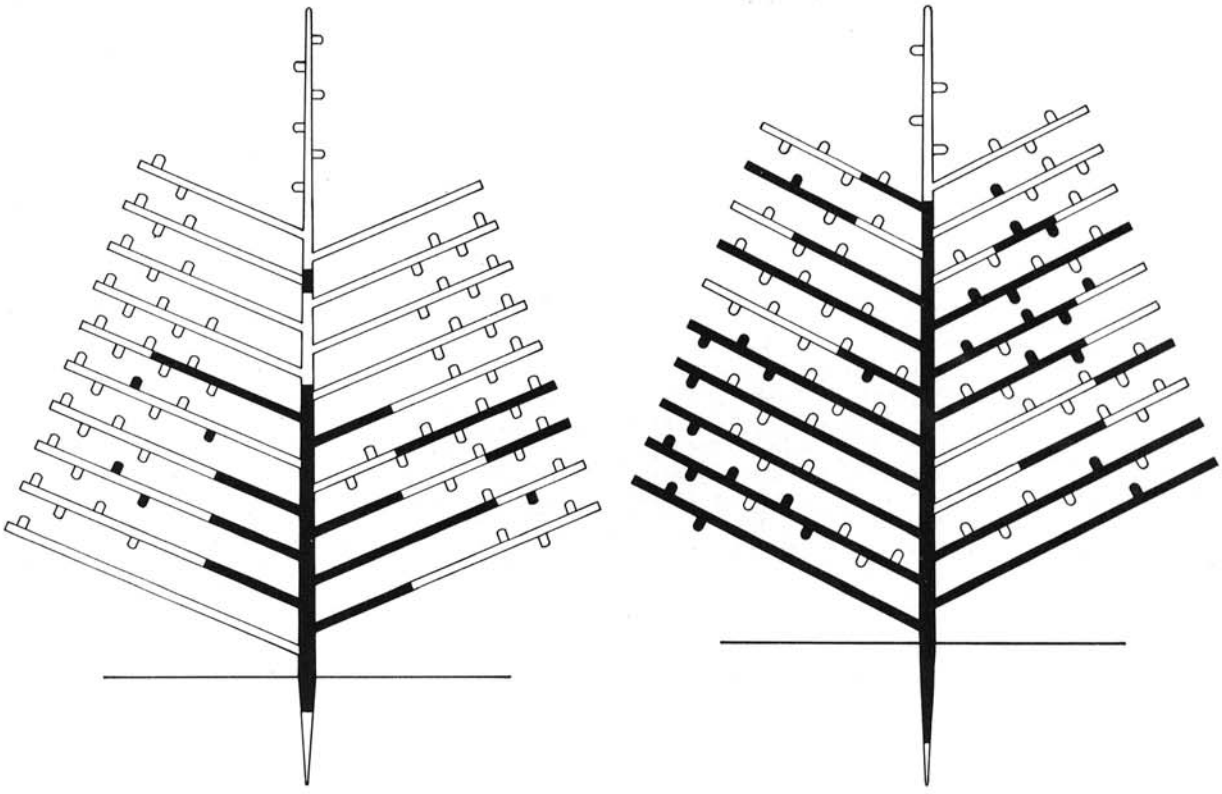

Fig. 11. Schemata showing in black the location of vascular infection by *Verticillium* in F_1 of two different wild Mexican × Upland cotton crosses.

conditioned to flower in a short-day regime for 60 days prior to transplanting. Each plant was scored in the field for symptoms of wilt at intervals of about 1 mo, and petioles were cultured for *Verticillium* as described previously (38).

The F_2 segregated for resistance and susceptibility to wilt in the ratio of approx. 3:1 (Table 1). Plants with the wilt score 1 developed slight or questionable symptoms of wilt; with scores 2 or 3, yellowing and dehiscence of a few or many, respectively, of the lower leaves; with score 4, severe symptoms, including stunting and general terminal dieback. Plants with score 5 were dead from wilt. Vascular discoloration was present in all plants; in those classed as resistant (scores 1 or 2) it was confined to the innermost wood, indicating that infection had occurred primarily when the plants were young. The plants preconditioned to flower were larger than the other seedlings when transplanted, and among them fewer plants than in the nonconditioned groups were susceptible.

DISCUSSION.—Our data indicate that *G. hirsutum* subsp. *mexicanum* var. *nervosum*, a wild, perennial, brown-fibered Mexican cotton of no agronomic value, is resistant to Verticillium wilt and, when crossed with Upland cottons, transmits the resistance to hybrids as a dominant factor. Though our progenies comprised small numbers of hybrids, the uniform, high resistance of the F_1 as determined by systematic, detailed culturing of plant

TABLE 1. Frequency array of wilt scores of F_2 plants of two cotton crosses (wild Mexican × Upland) transplanted as seedlings to the field. (F_1 plants were resistant)

Cross number	Wilt class					Ratio of resistant and susceptible plants
	Resistant			Susceptible		
	1	2	3	4	5	
BX833	5	15	6	6	4	26/10
BX833[a]	2	6	1	1	0	9/1
BX837	2	6	9	3	1	17/4
BX837[a]	4	1	0	0	0	5/0

[a]Seedlings were conditioned to flower by a short-day growing regime for 60 days prior to planting in the field.

Fig. 6-10. Localization of *Verticillium albo-atrum* in cotton plants by serial culturing. **6)** Wild Mexican cotton with leaves removed and branches numbered in preparation of serial culturing. **7-9).**Schemata showing in black the location of vascular infection in leaf petioles, branches, main stems, and roots as determined by culturing in October 1970. Hortizontal line indicates ground line and is equivalent to 80 cm. **7)** Acala SJ-1. Petioles were not cultured. **8)** Waukena White. **9)** Wild Mexicancotton. **10).**Vascular discoloration at base of main stems of cotton. Left to right: cultivars Acala SJ-1, Waukena White, and the wild Mexican cotton.

parts, and the predominant resistance of the F_2 nevertheless suggest a dominant monofactorial mode of inheritance and corroborate results of the extensive researches on this source of resistance reported in the USSR. Our data are also consonant with our previous thesis that resistance to Verticillium wilt derived from *G. barbadense* is inherited as a dominant factor in crosses with Upland cottons, but may show quantitative inheritance typical of certain polyploids (34). Our results should be viewed as showing only trends of inheritance, because segregation and variability in the F_2, including infertile plants and variables of field experimentation, made the scoring, particularly of susceptible plants with wilt scores of 3 or 4, a subjective process. Only plants with the wilt score 5 had clear-cut, severe terminal symptoms. Resistance may be associated more with the capacity of infected leaves to resist symptoms and dehiscence than with a capacity to localize infection in xylem tissues. Of the plants conditioned to flower by a short-day regime before transplanting to the field, fewer than expected showed wilt. This may, however, only reflect the fact that they were older and larger than the nonconditioned groups at the time of transplanting.

Resistance to Verticillium wilt of cotton now identified in wild *G. hirsutum* subsp. *mexicanum* var. *nervosum* and incorporated into successful commercial varieties in the USSR opens up many possibilities for augmenting the resistance level of our cotton varieties. Also the possibilities are good that there may be other untapped sources of resistance among wild *G. hirsutum*, some possibly closer to agronomic types than the wild Mexican cotton. These possibilities are under investigation.

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