Differential Effects of the Defoliating and Nondefoliating Pathotypes of *Verticillium dahliae* Upon the Growth and Development of *Gossypium hirsutum*

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ABSTRACT

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The effect of time of inoculation with either the defoliating (T9) or nondefoliating (SS4) pathotypes of *Verticillium dahliae* Kleb. upon the growth and development of upland cotton (*Gossypium hirsutum*, cultivar Acala SJ-2) was studied in the San Joaquin Valley of California in 1977 and 1978. Approximately 2,000 plants were stem-puncture inoculated at three different stages of growth in a 0.9-hectare field plot. Plant growth analysis in terms of plant heights, number of main stem nodes, squares, and bolls was made weekly throughout the growing season. In addition, fresh and dry weights of plant components were determined for biomass analysis. Data were also collected on the effect of the pathotypes upon seed cotton yields and fiber quality. Reduction of leaf dry matter accumulation was the plant component most affected by inoculation with *V. dahliae*. The defoliating pathotype had greater effects upon plant growth and development and seed cotton yields at all inoculation times than did the nondefoliating pathotype. Cotton plants inoculated with either pathotype of *V. dahliae* compensated for reduced photosynthate supply by reduction of fruiting load characteristic of uninfected plants under stress conditions.

Additional key words: pathobiology, plant growth analysis.

Verticillium wilt is a limiting factor in the production of cotton (*Gossypium hirsutum* L.) in some areas of the San Joaquin Valley of California. Since the first report of Verticillium wilt of cotton in California by Shapovalov and Rudolph in 1930 (23), the disease has caused variable losses. In recent years, average yield reductions of 3–7% have been reported, with 100% loss in some fields (8). Cultural practices, environmental conditions, and the concentration of propagules of *Verticillium dahliae* Kleb. in soil influence the occurrence and severity of wilt.

Acala cultivars of cotton have been selected for tolerance to Verticillium wilt under field conditions in the San Joaquin Valley where relatively high summer temperatures are common. Soil and air temperatures >30 C suppress foliar symptom development (2,3,12). However, at air temperatures of ≤26 C, all known cultivars of *G. hirsutum* are usually susceptible to wilt (28). Reduction of soil temperatures following irrigation often favors the

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development of wilt symptoms. Plant responses to infection by *V. dahliae* are markedly altered by postinoculation soil and air temperatures. Brinkerhoff (4) found that inoculated plants held in growth chambers with high day and low night temperatures were more resistant than those kept at a constant 27 C. Also, Barrow (1) demonstrated that tolerance would be induced in otherwise susceptible cotton cultivars by holding them at 27 C for 72 hr after inoculation.

In the early 1960s, a new pathotype of *V. dahliae* that caused severe defoliation in Acala cotton was reported by Schnathorst and Mathre (20). They also determined the host range and disease reaction of this pathotype in several cotton cultivars. Additional research (16,17,19,21) showed that the defoliating pathotype of *V. dahliae* occurs throughout the cotton-growing regions of the southwestern United States and in Central and South America.

Quantitative data on the effects of Verticillium wilt on cotton phenology and lint yields are sparse; however, some differences in pathogenesis of pathotypes of *V. dahliae* are known that include vascular occlusion (18) and changes in concentrations of growth regulators (27).

The purpose of this study was to analyze the effect of the defoliating (T9) and nondefoliating (SS4) pathotypes of *V. dahliae*

upon the growth and development and seed cotton yield of Acala SJ-2 cotton. These quantitative data were then used in the development of a model for Verticillium wilt that could be coupled to the UC SIMCOT cotton growth model (14,26).

MATERIALS AND METHODS

Field plots. Experimental plots were maintained during 1977 and 1978 at the West Side Field Station (WSFS), Five Points, CA. The Panoche clay loam soil at WSFS is representative of a wide area in the southern San Joaquin Valley. Conventional cultural and pest control practices usually followed in the area were used.

In 1977, data were recorded for seed cotton yields based on inoculation times of pathotypes while in 1978, the impact of pathotypes on plant growth and development as well as on seed cotton yields were determined.

The 0.9-hectare experimental plot consisted of three blocks subdivided into three subplots. Soil compaction and mechanical damage to plants were reduced by allocating a different subplot within each block for each inoculation time. The rows were oriented in an east-west direction on 96.5-cm centers and were 91.4 m long. The stand was thinned to 15–20 cm with a mean plant density of 6.3 ± 0.4 plants per meter of row producing a population of approximately 26,460 plants per hectare.

Soil assays for native *V. dahliae*. Determination of background levels of *V. dahliae* present within the field plots was made using the Andersen sampler method (5), as well as by isolation from diseased plants.

Leaves with foliar symptoms of Verticillium wilt were collected from uninoculated plants for determination of the indigenous pathotypes. Isolates of *V. dahliae* were established by grinding petioles of infected leaves in 10 ml of sterile distilled water, then plating 100-μl aliquots of a 1:10 dilution of the suspension on Ohio agar (24).

Pathogenicity characteristics of the isolates of *V. dahliae* were determined in temperature-controlled (21 C) greenhouse tests by using 6-wk-old Acala SJ-2 cotton plants grown in a mixture of Yolo loam and river sand (1:1, v/v). Conidial suspensions of the isolates were prepared from each of 20 cultures of *V. dahliae* derived from the infected plant material. Six plants were inoculated with three 20-μl droplets at 10^7 conidia per milliliter via stem-puncture for each isolate. All plants were rated for disease symptoms 21 days after inoculation.

Field inoculation. Randomly selected healthy plants were stem-puncture inoculated with a conidial suspension of either the defoliating T9 strain or nondefoliating SS4 strain. Control plants were injected with sterile distilled water. Inoculated plants were separated by approximately 3 m within the rows. Treatments were made on days 50, 70, and 90 postplant roughly corresponding to pre-squaring, first bloom, and peak bloom, respectively. Inoculum concentrations were adjusted upward according to plant age, from 2×10^4 for the first inoculation to 10^5 and 10^6 conidia per milliliter for the later inoculations. Inoculations were made within 5–10 cm of the soil line with a modified B-D autopipette (Becton-Dickinson, Rutherford, NJ 07073) fitted with a 0.81-mm-diameter (20-gauge) noncoring (Huber) needle.

Plant growth analysis. Plant growth analysis commenced 14 days after each inoculation time. Plant height, number of squares, and number of bolls were determined in the field until approximately 75% leaf canopy closure was achieved. Concurrent measurements were made on the weekly samples obtained for biomass accumulation data.

Five randomly selected plants from each treatment group at each inoculation time were sampled from each of the three blocks. Gross fresh weights were obtained on bulk samples (five plants per block per treatment) and the plants were partitioned into leaves, stems, roots, squares, and bolls. Fresh weights were obtained for each of the components prior to drying at approximately 50 C for at least 5 days in a forced air oven (7) for determination of dry weight.

Yield data were obtained by hand-picking seed cotton from all open bolls on 15 randomly selected plants from each block for each treatment and inoculation time. One-hundred-gram samples of seed cotton for each treatment and inoculation time were subjected to standard fiber quality analysis tests. Germination tests were conducted on the mechanically delinted seed derived from each treatment.

Root-shoot tissue density determination. In the course of deriving fresh and dry weights for the plant samples, it became apparent that there might be a difference in tissue density between samples from the different treatments following inoculation at day 50. This hypothesis was tested by deriving density data at days 92 and 196 during the season.

A 5-cm portion of root tissue immediately below the soil line was obtained from 15 randomly selected plants. The tissue samples were washed free of soil prior to drying at 50 C for 12 hr. The sample volume was measured by displacement of a mercury column within a 50-ml graduated cylinder. Weights were recorded to the nearest 0.01 gm and the tissue density (grams per cubic centimeter) derived.

Determination of physiological times. Air temperatures were recorded daily at the West Side Field Station through the 1977 and 1978 seasons. Physiological time was derived after the method of Gilbert and Gutierrez (13) based upon a threshold temperature of 11.9 C (53.5 F). The daily heat units are accumulated over the season and expressed as degree days (D°). Additional data concerning the use and derivation of degree days may be found in Gutierrez et al (14) as well as in Wang et al (26) and in Campbell et al (7).

RESULTS

Soil assays for native *V. dahliae*. Soil assays indicated a range of approximately four to 14 propagules of *V. dahliae*/g of soil along the drainage gradient of the experimental field. The northern (wetter) end of the field had a higher background count of *V. dahliae* propagules than the drier southern end. Foliar symptoms were observed in 14–27% of the uninoculated control plants by the end of August.

Natural pathotypes of *V. dahliae* in the experimental field. Pathogenicity tests using 20 naturally occurring isolates of *V. dahliae* derived from uninoculated plants were made under temperature-controlled greenhouse conditions with a 16-hr light and 8-hr dark cycle. Two of the 20 isolates caused extensive defoliation of the Acala SJ-2 plants within 21 days. Thus, the predominant pathotype of *V. dahliae* present within this group of isolates was the nondefoliating or SS4 type.

Plant inoculation. Inoculations of *V. dahliae* by the stem-puncture method produced a high incidence of uniform wilt symptoms within 3–5 wk. Foliar symptoms developed sooner and progressed more rapidly in the T9-inoculated plants than in those inoculated with SS4. In many instances leaves on plants inoculated with T9 progressed from chlorosis to complete dryness and abscission without displaying intermediate necrotic symptoms. Complete defoliation was not observed on any of the T9-inoculated plants at either time period, although pronounced stunting and marked defoliation was observed.

Vascular discoloration was noted in all plants inoculated with either T9 or SS4. The plant canopy within the two adjacent inoculated rows was considerably less dense in the T9 group than in either the SS4 group or healthy check plants.

In 1978, the first inoculations with conidial suspensions of *V. dahliae* were made at day 50 (June 23) when the plants were approximately 23 ± 2 cm tall (10–11 true leaf stage) following accumulation of 917 D°. Over 900 plants were inoculated to provide a homogenous population of infected plants from which to draw a representative sample. The air temperature did not exceed 32 C during the 10 days following inoculation. Mean daily maximum air temperature over this time period was 30.5 ± 1 C.

Epinasty was prominent within 7 days in all plants inoculated with T9. Epinasty also was apparent in plants inoculated with SS4 although the incidence was variable.

In comparison with healthy plants, a reddish-purple color in a darker green leaf developed 14 days after inoculation of plants inoculated with T9 and SS4. The phenomenon was transient and

was not clearly visible by 21 days postinoculation. Garber (11) reported a similar phenomenon following root penetration by *V. dahliae*. This physiological response of the host was not noted following inoculation at days 70 or 90.

Stunting was noted within 3 wk following the first inoculation; it was more pronounced and less variable in plants inoculated with T9 than in those of the SS4 group and healthy plants.

The second inoculation was made 3 wk later on day 70 (14 July) after accumulation of 1,326 D°. Mean plant height was 63 ± 1 cm while 16 ± 1 true leaves had formed. Maximum air temperature

recorded during the 10 days following the second inoculation was 40.6 C with a mean air temperature over this period of 38 ± 2 C.

Epinasty was observed within 21 days after inoculation in both the T9 and SS4 treatment groups. Foliar symptoms were visible in approximately 30% of the T9 inoculated plants, and to a lesser extent, in the SS4 group. After 5 wk, nearly 100% of the inoculated plants in both treatment groups displayed foliar symptoms.

The third inoculation of approximately 450 plants was made on crop day 90 (4 August). Accumulation of 1,982 D° had produced cotton plants 111 ± 4 cm tall with approximately 19 true leaves. The plants inoculated were in the early stages of boll set. Air temperatures during the day remained above 39 C for 7 days after inoculation with a mean temperature of 41 ± 1 C.

Foliar symptoms did not develop for several weeks. Stunting was noted prior to the development of chlorotic patches in many plants in the group inoculated with T9. After 5 wk, nearly 100% of the plants in the T9 group showed foliar symptoms whereas chlorosis was evident in only 60–65% of the plants in the SS4 inoculated group.

Plant heights. Stunting was apparent at the first sampling time (14 days) following the presquaring inoculation with both T9 and SS4. Mean plant height was 17% (7.5 cm) less for plants inoculated with T9 and 12% (5.0 cm) less for plants inoculated with SS4 than those of healthy control plants. By the end of September, those inoculated with T9 had 36% less plant height (43 cm), while those inoculated with SS4 or inoculated later with either T9 or SS4 were not significantly different from control plants (Table 1). Analysis of variance of the number of main stem nodes showed that only the presquaring inoculation with T9 caused a significant reduction by the end of the season.

The predominant cause of stunting of *V. dahliae* infected Acala SJ-2 cotton plants was reduced internode elongation rather than reduction in the initiation of new terminal nodes.

Total biomass. The effect of the defoliating and nondefoliating pathotypes of *V. dahliae* upon growth and development of Acala SJ-2 cotton was influenced by the age of the plant at the time of inoculation as well as by environmental conditions. Inoculation at presquaring (day 50) caused a proportionately greater effect upon subsequent growth, dry matter accumulation, and seed cotton yield than did the later inoculations (Fig. 1, Table 1). Plants inoculated at presquaring (day 50) with T9 showed greater total biomass reductions than did those inoculated with SS4. Plants inoculated with T9 had less total biomass than did those inoculated with SS4 when inoculation was at peak bloom, but not at white bloom (Fig. 1). The third inoculation made at day 90 postplant was immediately followed by a period of exceptionally hot weather. The high temperatures probably inhibited the development of *V. dahliae* within the host (4,12) and lessened the effect of the infection on plant development.

Dry matter accumulation in leaves. Dry matter accumulation in leaves was the plant component most affected by inoculation with *V. dahliae* pathotypes in 1978. Inoculation with T9 on day 50 resulted in a 54% reduction, while SS4 caused 39% reduction in leaf
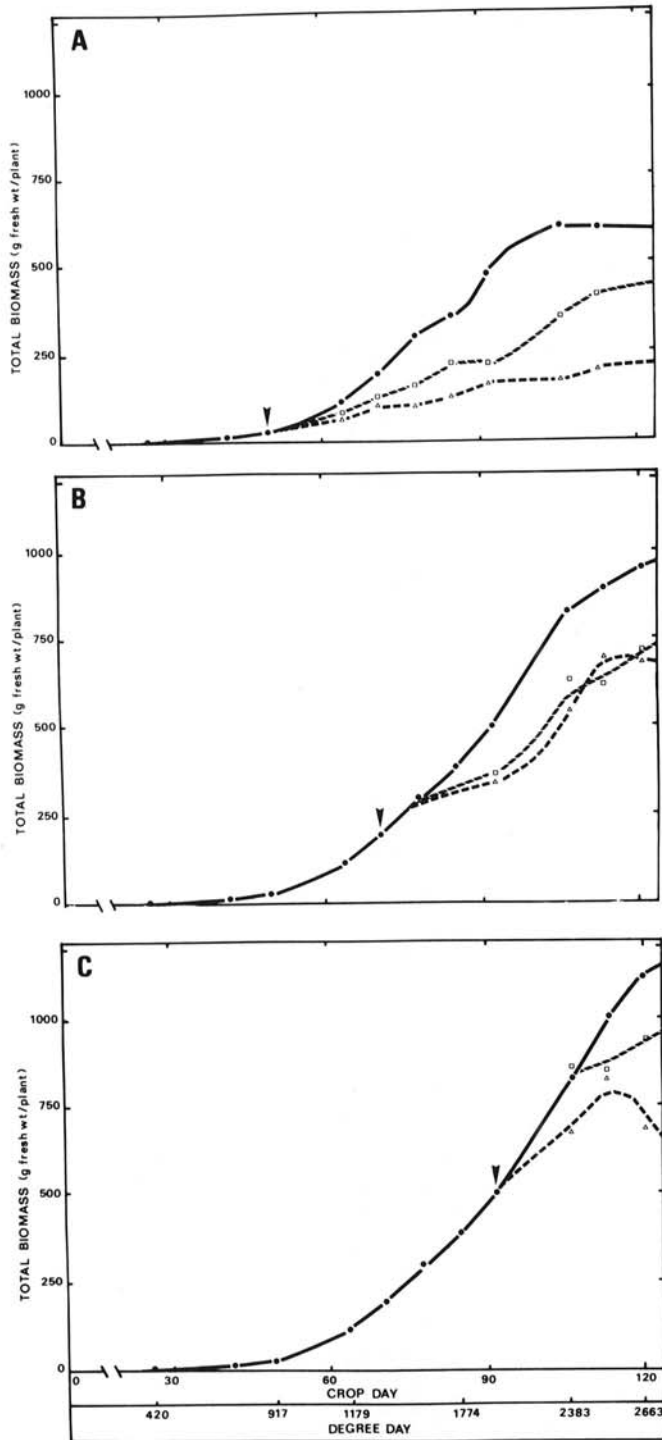

Fig. 1. Total biomass per plant following inoculation with different pathotypes of *Verticillium dahliae*. **A,** At day 50. T9 (defoliating) (△); SS4 (nondefoliating) (□); and water control (●). Arrow indicates time of inoculation. **B,** At day 70. T9 (△); SS4 (□); and water control (●). Arrow indicates time of inoculation. **C,** At day 90. T9 (△); SS4 (□); and water control (●).

TABLE 1. Effect of *Verticillium dahliae* pathotypes and inoculation times on growth and yield of Acala SJ-2 cotton in 1978

Inoculation time	Isolate[a]	Plant height (cm)	Bolls per plant	Seed cotton (kg/ha)
Presquaring,	T9	76 z[b]	2.8 z	252 z
day 50	SS4	102 y	6.7 yz	565 y
	Control	119 xy	19.0 uv	1,101 w
First bloom,	T9	105 xy	9.6 xy	727 xy
day 70	SS4	112 xy	12.6 wx	864 x
	Control	119 xy	15.5 vw	1,181 w
Peak bloom,	T9	125 x	15.6 vw	659 xy
day 90	SS4	120 xy	16.9 uvw	1,093 w
	Control	124 x	20.5 u	1,113 w

[a]Isolate T9 is the defoliating pathotype; SS4 is the nondefoliating pathotype.

[b]Numbers followed by the same letter within a column are not significantly different $P \leq 0.05$, according to Duncan's multiple range test.

dry matter compared to water-treated control plants.

Effect upon square formation. The onset of squaring was not delayed due to presquaring inoculation with either pathotype of *V. dahliae* (Fig. 2). Squaring began approximately by day 56–64 (1,000–1,100 D°). Peak squaring occurred in all treatments, as well as controls, by day 106.

The number of squares was significantly lower ($P \leq 0.05$) on plants inoculated with T9 or SS4 compared to controls within 21 days following inoculation at day 50. Reduction of square number was not significantly different in T9 and SS4-inoculated plants by day 70, but greater reduction occurred in T9-inoculated plants at later times.

Inoculation by day 70 with T9 resulted in a significant reduction in square numbers by day 85 when compared to either SS4 inoculated plants or control plants. Mean square count was 19.9 ± 2.8 in the T9 group, 25.9 ± 3.7 with SS4, and 28.7 ± 1.0 with control plants.

Inoculation at day 90 with T9 caused a significant ($P \leq 0.05$) 36% drop in square number when compared to control plants, while corresponding inoculations with SS4 resulted in a 12% decrease.

Boll load and relative fruitfulness. Green bolls first appeared in the control group by day 78 (1,555 D°) and steadily increased to a maximum boll count of 22.6 ± 3.5 by day 120 (2,663 D°) as a composite mean for all control plants (Fig. 3).

Inoculation with T9 or SS4 on day 50 resulted in a significant reduction in boll numbers (Table 1). The reduction was due primarily to inhibition of square formation and square shedding rather than boll shed. Only the inoculation at day 50 (presquaring) caused a consistent reduction in the index of fruitfulness (number of bolls per 100 g fresh wt [10]) during the remainder of the season. Inoculation at day 70 (first bloom) resulted in an apparent increase in fruitfulness until day 120 compared to the control group; fruitfulness index values were identical in all groups by day 120.

Another related measure of partitioning of available photosynthate between source and sink is the relative boll load (grams [fresh weight] of bolls per 100 g total plant biomass [fresh weight]). Inoculation at presquaring (day 50) with both T9 and SS4 caused the greatest impact of the three inoculation times. At the end of August (day 113), the T9-infected plants had 25% less fresh weight boll load than the control group, while the SS4 inoculated group was reduced 3.5%. The second and third inoculations on days 70 and 90 with either T9 or SS4 did not cause a significant reduction in the proportion of fresh boll weight to total biomass.
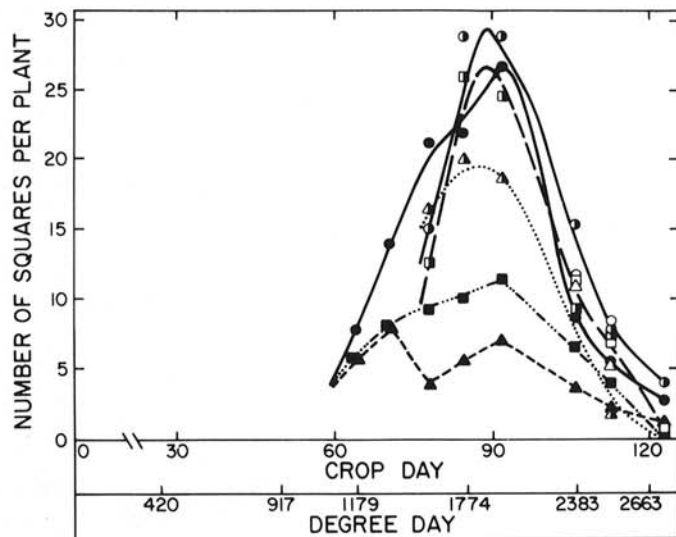
Root tissue density. Plants inoculated with T9 at day 50 had a mean root tissue density 8% greater than the control group by day 92. The difference was statistically significant ($P \leq 0.05$). Plants inoculated with SS4 or with T9 at day 70 or day 90 were not statistically different from the controls.

Seed cotton yields. In 1977, seed cotton yield was significantly reduced by T9 at both inoculation times (day 90 and day 110) compared to yields of water-treated controls (Table 2). Seed cotton yield also was significantly reduced by inoculation with SS4 on day 90, but not on day 110. Plants inoculated with SS4 at day 90 produced 16% less seed cotton than control plants, whereas plants inoculated with T9 produced 19% less. Inoculation with T9 at day 110 caused a 25% reduction in seed cotton weight.

In 1978, inoculation with T9 at day 50 resulted in a 77% decrease in seed cotton yield while SS4 caused a 49% reduction in yield when compared to healthy control plants. Inoculations at white bloom (day 70) with T9 caused a 38% yield decrease while SS4 reduced seed cotton weight by 27% (Table 1).

The significance of pathotypes in reducing lint yields was further shown by inoculations made at peak bloom (day 90). T9 caused a 42% yield reduction, while SS4 reduced seed cotton weights by 3.5% compared to healthy controls.

Fiber quality. Results of standard fiber quality analyses (25) made at the USDA Cotton Research Station, Shafter, CA, showed that inoculations made at day 70 or day 90 in 1978 with T9 caused a reduction in micronaire values when compared to SS4-inoculated or the control plant groups. Fiber fineness is correlated with maturity; lower micronaire values reflect a higher percentage of

TABLE 2. Effect of *Verticillium dahliae* pathotypes T9 and SS4 and inoculation times on seed cotton yields of Acala SJ-2 cotton in 1977

Inoculation time	Seed cotton yields (kg/ha)		
	T9 (defoliating)	SS4 (nondefoliating)	Control (sterile dH₂O)
Crop day 90 (1,579 D°)	1,095 ± 91 y	1,133 ± 153 y	1,347 ± 65 x
Crop day 110 (2,133 D°)	1,050 ± 80 y	1,303 ± 97 z	1,397 ± 71 x

ᵃ Values followed by different letters corresponding to each crop day are significantly different: crop day 90, $P \leq 0.01$ (*t*-test); crop day 110, $P \leq 0.05$.
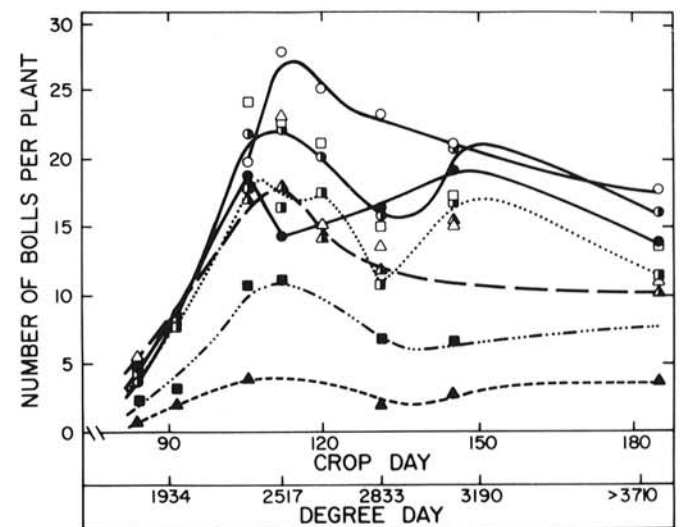

Fig. 2. The effect of pathotypes of *Verticillium dahliae* and time of inoculation on number of squares per cotton plant. Inoculated at day 50 with T9 (defoliating) (▲); T9 at day 70 (▲); T9 at day 90 (△). Inoculated at day 50 with SS4 (nondefoliating) (■); SS4 at day 70 (▣); SS4 at day 90 (□); check plants injected with distilled water at day 50 (●); water at day 70 (◐); and water at day 90 (○).

Fig. 3. The effect of pathotypes of *Verticillium dahliae* and time of inoculation on cotton boll development. Inoculated at day 50 with T9 (defoliating) (▲); T9 at day 70 (▲); T9 at day 90 (△). Inoculated at day 50 with SS4 (nondefoliating) (■); SS4 at day 70 (▣); SS4 at day 90 (□); check plants injected with distilled water at day 50 (●); water at day 70 (◐); and water at day 90 (○).

immature fibers within the bolls at harvest. Immature fibers are an apparent result of a slower growth and maturation rate.

Values for 50% span length were also reduced significantly by inoculation with T9 at day 90. This parameter is a measure of fiber length and further reflects growth rate differences between Verticillium-infected and healthy cotton plants.

Seed quality. Standard seed quality tests based upon germination percentages revealed no significant differences among any of the treatments at any of the inoculation times. All seed tested was of high quality with greater than 98% germination.

DISCUSSION

The effect of Verticillium wilt on growth and development of cotton plants depends on pathotype, host plant development at the time of infection, and postinoculation soil and air temperatures.

The rate of accumulation of total biomass in field grown cotton plants for each treatment reflects the effect of time of infection as well as pathotype. High air temperatures (40 C) following inoculation at days 70 and 90 may have arrested wilt development and allowed plants to partially recover. The defoliating T9 strain will grow on culture media at temperatures of 28–30 C. In contrast, growth of the nondefoliating SS4 pathotype is markedly reduced above 28 C (9). This differential sensitivity of the strains at temperatures normally encountered in the field may account for their different effects upon the total biomass accumulated in inoculated plants.

There are few reports of plant growth analysis following infection with *V. dahliae*. Selman and Pegg (22) examined leaf, stem, and root dry matter accumulation in tomato plants inoculated with *V. albo-atrum* and found that the rate of dry matter accumulation in leaves was the plant growth parameter most affected. They also observed stunting prior to foliar symptom development following inoculation with *V. albo-atrum*.

In the present study, rate of leaf dry matter accumulation was also the growth parameter most affected by infection with *V. dahliae*. Rate of leaf dry matter accumulation was reduced 54% by T9 and 39% by SS4 when inoculations were made at day 50. In contrast, Harrison and Isaac (15) found no decrease in the number of leaves on the main stem axis of potato plants inoculated with *V. albo-atrum* or *V. dahliae*, although they reported a reduction in the number of leaves on lateral stems.

The primary factor resulting in lower boll counts in plants infected by *V. dahliae* appears to be reduced square formation and higher square shed rate rather than direct boll shedding. Very young bolls (<5 days old) are also shed. Reduced square formation is related to a reduction in fruiting point initiation as a result of a reduction in lateral branch elongation. This phenomenon appears to be directly responsible for the impact of infection by *V. dahliae* upon seed cotton yields.

Eaton (10) previously studied carbohydrate utilization in the cotton plant as it is affected by various agronomic variables. His findings showed that the developing boll is the strongest sink for photosynthate production. Partitioning further, Eaton found that maturation of seed was the highest priority of the plant. Gutierrez et al (14) found that Acala cotton (SJ-2) responded to imbalances in photosynthate supply and demand by shifting priority to boll maturation. Compensation for reduced photosynthate supply results in reduced boll set until a balance with supply is achieved. The present study confirmed this phenomenon in relation to Verticillium wilt. Derivation of the index of fruitfulness following inoculation with either T9 or SS4 at days 50, 70, and 90 revealed a striking similarity in boll-carrying capacity among all treatments and time periods. The derived boll load values for the different treatments indicate that the Acala SJ-2 cotton variety is remarkably resilient in balancing fruit load (reproductive) and total biomass (vegetative) growth in response to stress conditions. Acala SJ-2 cotton inoculated with either pathotype of *V. dahliae* exhibited compensation and adjustment of fruit load characteristic of normal photosynthate supply and demand functions under stress conditions (14).

Seed germination tests also confirm Eaton's (10) findings that the developing seed is the strongest nutrient sink. All seed derived from plants inoculated with either T9 or SS4 at days 50, 70, and 90 had >98% germination. No significant difference in seed weight or seed number was observed in any of the treatments.

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