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The influence of verticillium wilt epidemics on cotton yield in southern Spain

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Experiments were conducted in the Guadalquivir Valley of Andalucía, southern Spain, in 1986 and 1987, using field plots naturally infested with different inoculum densities of the defoliating and nondefoliating pathotypes of *Verticillium dahliae* to determine the influence of verticillium wilt epidemics on yield of cotton cultivar Coker 310. The total number of bolls, the number of open bolls, and seed cotton yield were related to the growth stage of plants at first appearance of foliar symptoms, and to inoculum density and virulence of the *V. dahliae* pathotype prevailing in the soil. For the three yield components, the greatest reduction was observed in plants showing symptoms before opening of first flowers (about 650 degree-days after sowing). Yield increased with delay in the development of foliar symptoms during the crop season, and the effect of the wilt epidemics on yield was small or nil for plants that developed symptoms after opening of the first bolls (1400–1500 degree-days after sowing). A multiple regression equation was derived that related yield reduction to the physiological time accumulated from the time of sowing until the appearance of foliar symptoms and to the rate of disease intensity increase over physiological time. This multiple point model explained about 70% of the variation in cotton yield loss due to verticillium wilt.

INTRODUCTION

About 83 000 ha of upland cotton (*Gossypium hirsutum*) are grown in the Guadalquivir Valley, Andalucía, southern Spain, accounting for *c*. 94% of the national cotton acreage in Spain (Anonymous, 1993). In this area, verticillium wilt, caused by *Verticillium dahliae*, is widespread and is now considered to be the most important disease of the crop. Disease surveys in the area in 1981–1983 and 1985 indicated that 80–82·5% of fields were affected, with a mean incidence of diseased plants of approximately 20% (Bejarano-Alcázar *et al*., 1996). Incidence and severity of attacks by the disease were higher in the Lower Valley, in which high inoculum densities of a cotton-defoliating pathotype of *V. dahliae* prevail (Bejarano-Alcázar *et al*., 1996).

Verticillium wilt inhibits growth and development of cotton, causing a reduction of biomass, internode length, development of squares and bolls, number of open bolls and fibre production (Friebertshauser & DeVay, 1982; Pullman & DeVay, 1982b). Furthermore, the length, strength and fineness of fibre produced by diseased plants may be reduced (Bugbee & Sappenfield, 1970; Friebertshauser & DeVay, 1982). Most of these effects can be detected *c*. 2 weeks before foliar symptoms, indicating that the time to foliar symptoms development is a yield-determinant factor for the crop (Friebertshauser & DeVay, 1982; Pullman & DeVay, 1982b). On the contrary, the incidence of infections, as indicated by the occurrence of vascular discoloration, has little effect on yield (Bassett, 1974; Ashworth *et al*., 1979). Incidence of verticillium wilt foliar symptoms is highly influenced by inoculum density and the virulence of *V. dahliae* pathotypes prevailing in soil, as well as by air and soil temperature and cultivar tolerance (Ashworth *et al*., 1979; Pullman & DeVay, 1982a; Paplomatas *et al*., 1992; Bejarano-Alcázar *et al*., 1995). Thus, for a given inoculum density, epidemics caused by the defoliating pathotype of *V. dahliae* develop earlier and more rapidly than those caused by the nondefoliating pathotype (Bejarano-Alcázar *et al.,* 1995). Therefore, the defoliating pathotype may induce a larger effect on all

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cotton growth parameters and yield of affected plants as compared to the nondefoliating one (Friebertshauser & DeVay, 1982).

The objective of this study was to determine the influence of epidemics of verticillium wilt developed from different inoculum densities of the cotton-defoliating and nondefoliating pathotypes of *V. dahliae* on yield components of cotton under conditions in the Guadalquivir Valley. Results from that part of the study dealing with the epidemiological aspects have been reported elsewhere (Bejarano-Alcázar *et al*., 1995).

MATERIALS AND METHODS

General description of the experimental fields

Experiments were conducted in 1986 and 1987 in selected field plots at several locations of the Guadalquivir Valley with a history of verticillium wilt of cotton. Soil in these fields was known to be naturally infested to various degrees with either the defoliating or nondefoliating pathotypes of *V. dahliae* or both. A sample of monoconidial isolates of the pathogen was obtained from affected cotton plants in each plot in the previous year (Bejarano-Alcázar *et al*., 1995). These isolates were used to characterize the pathotypes prevalent in each field by means of the morphology of microsclerotia, the differential growth on sanguinarine-amended potato-dextrose agar, and pathogenicity tests on cotton cultivars (Presley, 1969; Schnathorst, 1973; Bejarano-Alcázar *et al.*, 1995).

In 1986, experimental plots were established in five fields (one 30×30 m plot per field) designated A–E. Fields A, B, C and E (vertic soil, about 62% clay, 0·9–1·4% organic matter, pH 7·8–8·8) were in the lower Valley (Sevilla province) while field D (loamy soil, 27% clay, 1·1% organic matter, pH 8·2) was in the higher Valley (Jaén province). In 1987, three plots of $7{\cdot}5 \times 10$ m and 4×10 m were established in each of fields A and B, respectively, and one plot of 20×15 m was located in field D. In both years, plots were sown to cotton cultivar Coker 310, which is highly susceptible to verticillium wilt (Blanco-López *et al.*, 1992), between mid-April and the beginning of May. Rows were 0·95 m apart (except 0·75 m apart for field D) with a plant stand thinned to $100–120 \times 10^3$ plants/ha. Seedbed preparation, cultivation, fertilization and irrigation were carried out according to farmers' practices in the area (Rodríguez & Carnero, 1991). Inoculum density of *V. dahliae* in the plots was determined in soil samples collected to a depth of 20 cm in each plot within 1 month of sowing, using the Andersen sampler method (Butterfield & DeVay, 1977; Bejarano-Alcázar *et al*., 1995). The inoculum density was expressed as the number of propagules per gram of dry soil (p/g).

Physiological time

Physiological time scales standardize the time component of plant development because they take into account environmental variables that may affect plant growth and epidemic progress. Daily maximum and minimum air temperatures were obtained from meteorological stations located near the experimental plots. The heat units, expressed as Celsius degree-days, were calculated for each 12-h interval by integrating the area enclosed under the line connecting the daily maximum and minimum temperatures among consecutive days and above 11·9°C (the developmental threshold temperature for cotton growth) (Gutierrez *et al*., 1975; Reddy, 1994), using a triangulation method (Sevacherian & El-Zik, 1983). Physiological time was determined as the cumulative number of degree-days from the time of sowing.

Disease development and plant growth

The incidence (%) of plants showing foliar symptoms of verticillium wilt (Schnathorst, 1981) and the severity of symptoms in each affected plant were determined per plot each year in a total of 300 plants. In 1986, 50 consecutive plants in each of six rows 5 m apart were inspected. In 1987, 75 consecutive plants in each of four adjacent rows and 100 consecutive plants in each of three adjacent rows were examined for each of the three plots of fields A and B, respectively. For the plot in field D in 1987, 100 consecutive plants in each of three rows 6 m apart were examined. Disease assessments were made at 7- to 14-day intervals from mid-June to mid-September, or until the incidence of foliar symptoms was 90–95%. Severity of symptoms was assessed on a 0 to 4 rating scale according to the percentage of plant tissue affected by acropetal chlorosis, necrosis, wilt and/or defoliation (0, healthy plant; 1, 1–33%; 2, 34–66%; 3, 67–99%; 4, dead plant) (Bejarano-Alcázar *et al*., 1995). A disease intensity index (D_I) was determined at each recording date by the equation: $D_I = (I \times S) \div M$, in which I and S are the incidence and mean severity of foliar symptoms, respectively, and M is the maximum (4) severity rating. D_I is a parameter more appropriate than incidence of foliar symptoms to compare disease severity among epidemics of verticillium wilt (Bejarano-Alcázar *et al*., 1995), as it expresses the mean disease intensity in the crop as a percentage relative to the maximum value attainable. Epidemics of verticillium wilt in the plots were characterized by the increase of D_I over physiological time accumulated from the time of sowing. At each disease assessment date, diseased plants were tagged to record the physiological time when foliar symptoms first appeared on these plants. At the time of harvest, between 27 September and 21 October each year, the number of total and open bolls in each plant was recorded, and seed cotton was hand picked from each group of plants with the same time to foliar symptoms appearance. The growth stages defined by Chiarappa (1971) are used throughout.

Analysis of data

Least squares regression analyses were performed to fit a straight line to data of D_I increase over physiological time (Draper & Smith, 1981; Campbell & Madden, 1990). Although other models were as appropriate as the straight line model to describe curves of D_I increase (Bejarano-Alcázar *et al*., 1995), the straight line model was chosen because it is the simplest and easiest to use. The rate of D_I increase over physiological time was estimated by the slope value of the regression line. Also, the area under the D_I progress curve (AUDPC) was calculated by trapezoidal integration between 0 and 1400 degree-days and expressed as a percentage of the maximum possible area for this period (Campbell & Madden, 1990).

For each experimental plot, the number of total and open bolls and the seed cotton yield were averaged per plant for each time to foliar symptoms appearance, and expressed as a percentage of values for symptomless plants at the final disease assessment (20–100 plants depending of the plot). The symptomless plants were chosen from the 300 used for disease records in a plot, or from other plants in the plot if that was not possible. In addition their variation with the physiological time of disease appearance was represented graphically and the relationship between these variables was examined. The relationship between the three yield components, the descriptive parameters of curves of D_I increase over time, and the physiological time to foliar symptoms development was analysed using the combined data from 1986 and 1987. Multiple regression equations were fitted to the data. The general form of the regression model used was:

$$Y = a + b_1X_1 + b_2X_2$$

where Y is the mean total number of bolls, mean number of open bolls, or seed cotton yield per plant, for each group of plants in which foliar symptoms of verticillium wilt were observed at the same recording date, expressed as a percentage of the mean value of the same variable in symptomless plants in each plot; X_1 is degree-days accumulated from the time of sowing until the appearance of foliar symptoms in each group of plants and plot; and X_2 is the rate of D_I increase over the physiological time, or AUDPC, in each experimental plot.

Regression analyses were performed with non-transformed data as well as with data transformed to decimal logarithms. Data on yield components were increased by 1·0 before log transformation to avoid zero values. Regression analyses were performed using the statistical package Statistix (Analytical Software, Roseville, MN, USA). The goodness-of-fit of data to models was assessed by the coefficient of multiple determination (r^2), the partial correlation coefficient for each independent variable, the F-statistic in the analysis of variance, the standard error of estimate of the dependent variable, the standard error and significance of the estimated parameters, and the pattern of residuals versus predicted Y values (Draper & Smith, 1981; Campbell & Madden, 1990).

RESULTS

Pathotypes of *V. dahliae* in the experimental fields

All the isolates of *V. dahliae* from fields A, B and C and 12% from E were of the highly virulent and cotton-defoliating type. All the isolates from field D and the other 88% of isolates from field E were characterized as moderately virulent and nondefoliating (Bejarano-Alcázar *et al*., 1995).

D_I increase over physiological time

Increase of D_I showed a significant ($P < 0{\cdot}05$) straight-line relationship with physiological time accumulated from sowing in both 1986 and 1987, with r^2 ranging from 0·84–0·99 among the experimental plots (Bejarano-Alcázar *et al*., 1995). Rates of D_I increase and AUDPC values ranged, respectively, from 0·053–0·118 and 12·5–39·0% for plots infested mainly with the defoliating pathotype of *V. dahliae*, and from 0·021–0·026 and 3·9–6·9% for plots infested with the nondefoliating pathotype (Bejarano-Alcázar *et al*., 1995).

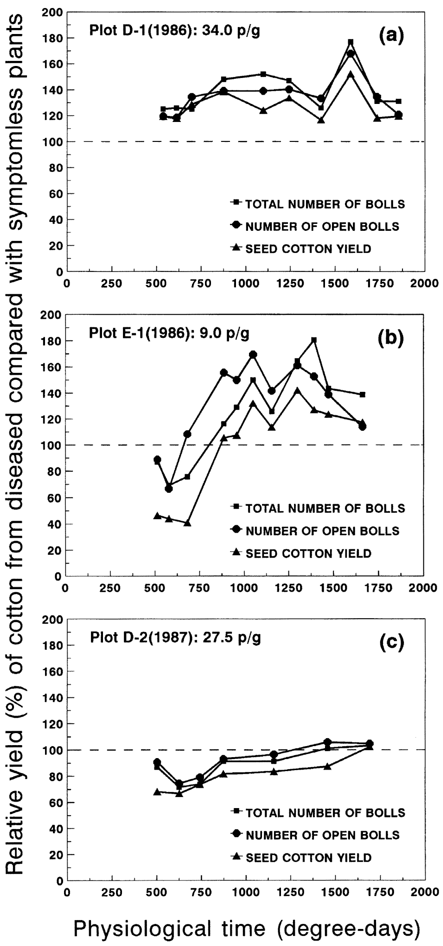

Fig. 1 Influence of physiological time to appearance of first foliar symptoms on yield components in cotton plants affected by verticillium wilt, in fields infested with different inoculum densities of the nondefoliating pathotype of *Verticillium dahliae* in southern Spain. The dotted line parallel to the time axis at the 100% point denotes yield equal to symptomless plants.

Effect of verticillium wilt development on cotton yield components

Figures 1–4 show the percentages of total bolls, open bolls and seed cotton yield from diseased cotton plants relative to those from symptomless plants, plotted against the physiological time to foliar symptoms appearance in the various experimental plots. Production in symptomless plants is represented as 100%.

The effect of verticillium wilt development on cotton yield varied with the pathotype and inoculum density of *V. dahliae*. In 1986, the three yield components (as above) in diseased plants were similar to, or higher than, those in symptomless plants for plots D-1 and E-1, which were infested respectively with high (34·0 p/g) or low (9·0 p/g) inoculum density of the nondefoliating pathotype (Fig. 1a, b). However, those plants in plot E-1 that showed foliar symptoms prior to the growth stage of first open flowers (650–750 degree-days after sowing) suffered yield loss. In these plants, seed cotton yield represented only 41–46% of that obtained in symptomless plants (Fig. 1b). In 1987, the rates of D_I increase over physiological time in plots located in the same experimental fields and infested with similar inoculum density of *V. dahliae* were higher than in 1986 (Bejarano-Alcázar *et al.*, 1995). Thus, the epidemic of verticillium wilt in plot D-2, with high inoculum density (27·5 p/g) of the nondefoliating pathotype, was more severe than that in plot D-1 in the previous year (final mean disease severity in the affected plants was 1·8 in 1987 and 1·3 in 1986). As a consequence, all three yield components in plot D-2 were reduced in plants showing foliar symptoms before the growth stage of first open bolls (1500–1700 degree-days). Development of foliar symptoms after 1500 degree-days did not affect yield (Fig. 1c). Yield reduction was related to the physiological time to appearance of foliar symptoms: the earlier the foliar symptoms developed the greater was the reduction for all yield components.

The correlation between the three yield components and the physiological time accumulated from sowing was much more noticeable in plots C-1, B-2, B-3 and B-4 (Fig. 2). These plots were infested with a low inoculum density (2·0–10·0 p/g) of the defoliating pathotype, and yield in them increased as development of foliar symptoms was delayed during the crop season until 1200–1800 degree-days (Fig. 2a–d). The effect of disease development on yield reduction in these plots was greater than in plots in which the nondefoliating pathotype predominated. All three yield components were almost nil in plants with foliar symptoms occurring at 450–650 degree-days, that is, between the growth stage of first flower bud squares and first open flowers (Fig. 2a–d). In plots A-1 to A-4, infested with a high inoculum density of the defoliating pathotype (44·0–75·5 p/g), there was a substantial reduction of all three yield components regardless of the time to foliar symptoms development (Fig. 3a–d). In plot B-1, infested with a moderately high level of inoculum of the defoliating pathotype (24·0 p/g), yield components were severely reduced in plants showing foliar symptoms before appearance

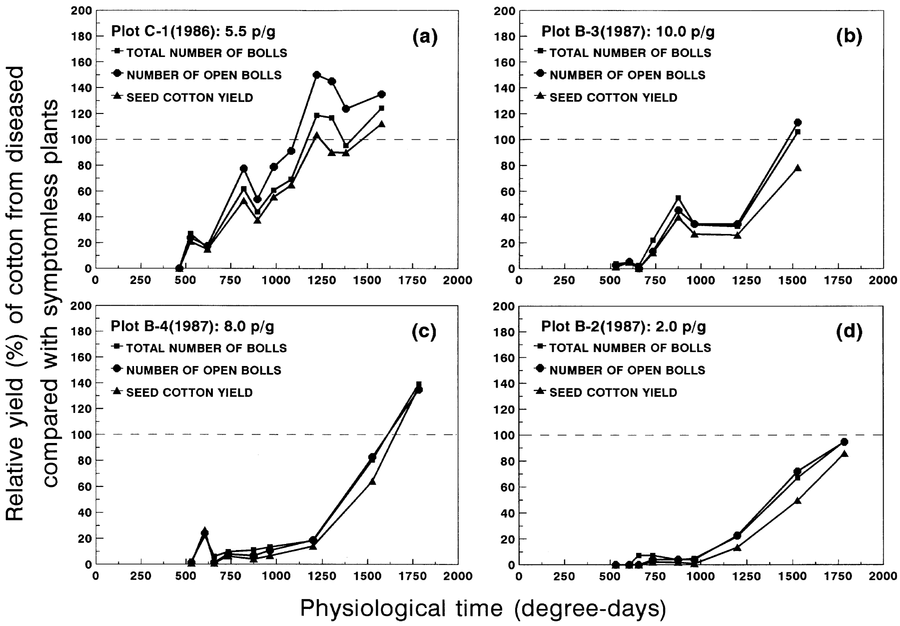

Fig. 2 Influence of physiological time to appearance of first foliar symptoms on yield components in cotton plants affected by verticillium wilt, in fields infested with low inoculum density of the defoliating pathotype of *Verticillium dahliae* in southern Spain.

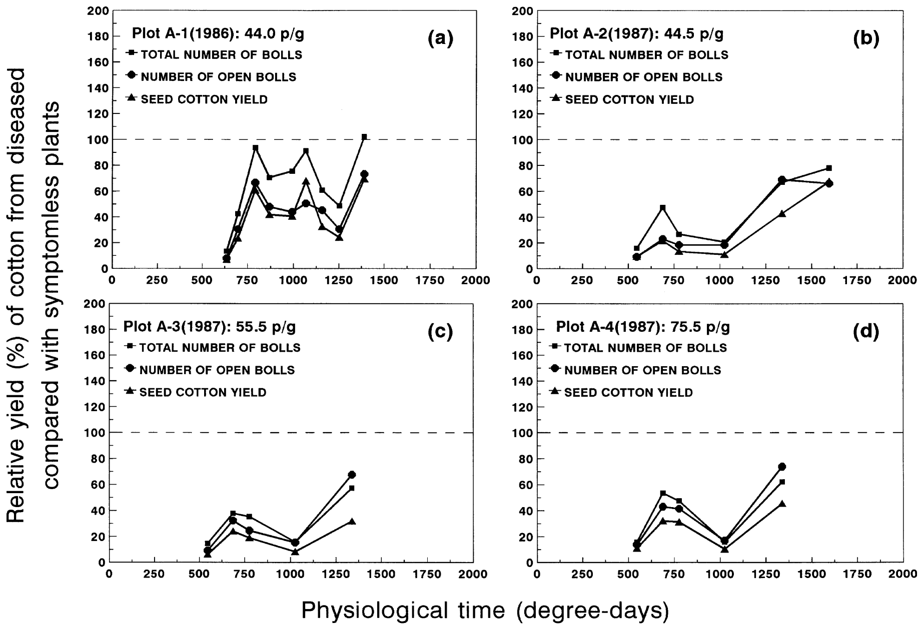

Fig. 3. Influence of physiological time to appearance of first foliar symptoms on yield components in cotton plants affected by verticillium wilt, in fields infested with very high inoculum density of the defoliating pathotype of *Verticillium dahliae* in southern Spain.

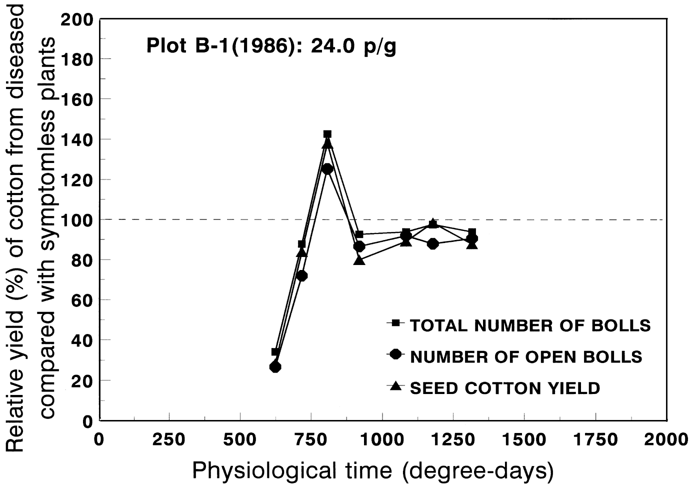

Fig. 4 Influence of physiological time to appearance of first foliar symptoms on yield components in cotton plants affected by verticillium wilt, in fields infested with moderately high inoculum density of the defoliating pathotype of *Verticillium dahliae* in southern Spain.

of the first open flowers (650 degree-days). However, this effect was less pronounced in plants for which symptoms of wilt developed later (Fig. 4).

Although all three yield components showed similar trends, seed cotton yield was the component more severely affected by the disease than the total number of bolls or the number of open bolls, in all experimental plots (Figs 1–4). The total number of bolls, number of open bolls, and average seed cotton yield per ha for each plot are shown in Table 1. In both 1986 and 1987, the three yield components were always higher in plots infested with the nondefoliating pathotype than in plots infested with the defoliating pathotype, except for the comparison of the number of open bolls in plot E-1 against the corresponding values in plots B-1 and C-1 (Table 1). This exception may be explained by the fact that plot E-1 was harvested 20 days earlier than the two other plots, and that it also contained a low proportion of defoliating strains. For comparison, mean seed cotton yield in nine selected disease-free plots in field B in 1987, indicative of the yield attainable in that field (Nutter *et al*., 1993), averaged 4832·7 kg ha^{-1}. This was about 1·8 × higher than the yield in plot B-2, and 4 × higher than that in plots B-3 and B-4. Similarly, in 1987, seed-cotton yield in a selected disease-free plot in field A was 2300 kg ha^{-1}, around 4 × the average yield of plots A-2, A-3 and A-4.

The time to foliar symptoms development also influenced the percentage of open bolls relative to the total number of bolls per plant. In plots E-1 and D-2, infested with a low or high inoculum density (9·0 and 27·5 p/g, respectively) of the nondefoliating pathotype, and in plot C-1, infested with a low inoculum density (5·5 p/g) of the defoliating pathotype, the percentage of open bolls was higher in diseased than in symptomless plants, indicating an earlier maturation of the crop induced by verticillium wilt. This effect was not apparent in plants that developed foliar symptoms either very early or at the end of the growing season, for which the percentage of open bolls was similar to that in healthy plants. However, in the other plots infested with low to high inoculum density of the defoliating pathotype, the percentage of open bolls in diseased plants was similar to or lower than that in the symptomless plants (Figs 1–4).

Forty-eight multiple regression equations were fitted to the combined data from the 1986 and 1987 field experiments. For regression analyses, yield components were the dependent variable and the physiological time accumulated to symptoms appearance and descriptive parameters of verticillium wilt epidemics were the independent variables. Both nontransformed and log transformed data were used for the analyses. Results of regression analyses indicated an overall highly significant ($P < 0·001$) relationship among those variables, as indicated by the *F*-test in the analysis of variance (94 d.f.), in all the models studied. Nevertheless, for the three yield components, the coefficient of multiple determination and the partial correlation coefficients were always higher, and the standard error of estimate of the dependent variable was lower, when the rate of D_I increase over the physiological time, rather

Table 1 Influence of verticillium wilt epidemics on yield components of cotton cultivar Coker 310, in fields with different inoculum densities of the defoliating and nondefoliating pathotypes of *Verticillium dahliae* in southern Spain

Year	Predominant pathotype and plot	Initial inoculum density[a] (p/g)	Total bolls (Number/ha) ($\times 10^3$)	Open bolls (Number/ha) ($\times 10^3$)	Seed cotton (kg ha^{-1})
1986	Defoliating				
	C-1	5·5	884·8	783·8	3376·0
	B-1	24·0	730·0	584·0	3103·2
	A-1	44·0	433·0	269·0	1190·0
	Nondefoliating				
	E-1	9·0	999·2	572·8	3674·7
	D-1	34·0	1390·3	1182·9	5476·5
1987	Defoliating				
	B-2	2·0	653·0	611·0	2637·0
	B-4	8·0	329·9	297·0	1204·6
	B-3	10·0	355·7	307·1	1203·0
	A-2	44·5	253·7	158·3	603·3
	A-3	55·5	202·3	134·3	451·7
	A-4	75·5	226·3	170·3	611·7
	Nondefoliating				
	D-2	27·5	875·9	840·8	3909·9

[a] Determined by the method of Butterfield & DeVay (1977). See text.

than AUDPC, was the parameter used as independent variable to describe the epidemics. The regression equation that provided best fit is:

$$Y = a + b_1 \operatorname{Log} X_1 + b_2 \operatorname{Log} X_2$$

where Y is the yield data expressed as the percentage relative to the mean of the yield component in symptomless plants, X_1 is the physiological time to first foliar symptoms (degree-days), and X_2 is the rate of D_I increase over physiological time accumulated from sowing.

This model explained 68·0, 70·9 and 67·7% of the variation in the total number of bolls, the number of open bolls and seed cotton yield, respectively (Table 2). There was no discernible pattern of the residual values of the regression equations when residuals were plotted against their respective predicted values. The partial correlation coefficients for X_1 and X_2 were, respectively, 0·630 and $-0{\cdot}731$ for the total number of bolls; 0·636 and $-0{\cdot}765$ for the number of open bolls; and 0·611 and $-0{\cdot}737$ for seed cotton yield. These results indicate a nonlinear variation of the three yield components, each of which increases as development of foliar symptoms is delayed, and decreases as the severity of the verticillium wilt epidemic increases.

DISCUSSION

The effect of verticillium wilt epidemics on the total number of bolls, number of open bolls, and seed cotton yield for the cultivar Coker 310 was related to the phenological growth stage of plants when foliar symptoms first developed, and to the amount and virulence of the *V. dahliae* pathotype prevailing in soil. The greatest reductions in the three yield components occurred in plants showing symptoms before opening of first flowers, approximately 650 degree-days after sowing, with yields increasing when development of foliar symptoms was delayed through the season. These results agree with those from other studies (Friebertshauser & DeVay, 1982; Pullman & DeVay, 1982b). In our work, seed cotton yield was affected by the disease more severely than the total number of bolls. This observation is consistent with the findings of Friebertshauser & DeVay (1982) and Pullman & DeVay (1982b), who showed that the primary contribution of infection by *V. dahliae* to cotton yield reduction is a reduced square formation and a higher square shed rather than boll shedding. Once bolls are set, they usually remain attached to the plant and continue to accumulate dry matter, although plants affected early in the season usually bear small bolls with

Table 2 Multiple regression equations that best describe the effect of physiological time to foliar symptoms appearance and the severity of verticillium wilt epidemics on yield components of cotton cultivar Coker 310 in southern Spain

Dependent variable[a]	Independent variable[b]	Intercept	Partial regression coefficient	Standard error of estimated parameters	t P value	Partial correlation coefficient	Standard error of dependent Variable	F P value	r^2 [c]
Total bolls	Log (X_1)	−495·86	142·79	18·16	0·0000	0·630	28·31	0·0000	0·680
	Log (X_2)		−112·12	10·78	0·0000	−0·731			
Open bolls	Log (X_1)	−516·31	144·35	18·07	0·0000	0·636	28·17	0·0000	0·709
	Log (X_2)		−123·38	10·73	0·0000	−0·765			
Seed cotton	Log (X_1)	−452·99	126·61	16·92	0·0000	0·611	26·37	0·0000	0·677
	Log (X_2)		−106·30	10·05	0·0000	−0·737			

[a] Yield component per plant for each time of foliar symptoms appearance and plot, expressed as a percentage of the respective values in healthy plants at the same plot.
[b] X_1, degree-days accumulated from sowing until the appearance of foliar symptoms in each group of plants and plot; X_2, rate of lineal D_I increase over physiological time.
[c] r^2, coefficient of multiple determination.

less cotton. As shown in our study, yield reduction was small or nil in plants that developed foliar symptoms after the first open bolls, *c*. 1500 degree-days after sowing. Similar critical times of 1330–1400 degree-days were reported in California (Pullman & DeVay, 1982b; Melero & DeVay, 1986). Pullman & DeVay (1982b) indicated that when foliar symptoms develop in plants undergoing fruit-load stress (photosynthate demand exceeding supply), their growth has already slowed down and the effect of verticillium wilt is often less severe.

However, our experiments show that epidemics may follow various courses depending on the virulence and inoculum density of the *V. dahliae* pathotype prevailing in soil. In a plot with high inoculum density (34·0 p/g) of the nondefoliating pathotype, the three yield components studied were always higher in diseased than in symptomless plants, regardless of the physiological time to foliar symptoms appearance (Fig. 1a). A similar relationship was found for the index of cotton fruitfulness (number of bolls per 100 g of fresh weight), which showed an apparent increase in field inoculations at first bloom with *V. dahliae* isolates (Friebertshauser & DeVay, 1982). A similar stimulation of cotton plant growth derived from light insect damage has also been demonstrated (Gutierrez *et al*., 1975). Conversely, in plots with very high inoculum density (44·0–75·5 p/g) of the defoliating pathotype, the total number of bolls, number of open bolls, and seed cotton yield were severely reduced for the majority of values of time to foliar symptoms development (Fig. 3). This detrimental effect of the defoliating pathotype, as compared to the nondefoliating pathotype of *V. dahliae*, confirms previous reports by other authors (Friebertshauser & DeVay, 1982).

Verticillium wilt of cotton also affects the ratio of current photosynthate availability by the plant to total demand by all of its developing parts. This ratio controls growth increments and priorities in cotton plants (Gutierrez *et al*., 1975, 1983; Gutierrez & DeVay, 1986). When carbohydrate stress occurs, leaf, stem and root growth are slowed down considerably, and the plant switches to a boll maturation phase (Gutierrez *et al*., 1975). Melero & DeVay (1986) found that in plots infested with 8–22 p/g of the defoliating pathotype of *V. dahliae* the percentage of open bolls per plant was lower for symptomless plants than in diseased plants and increased as time to appearance of foliar symptoms decreased, indicating an earlier maturation in diseased plants. In our study, this effect was observed only in plots with low or high inoculum density of the nondefoliating pathotype, and in one plot with low inoculum density of the defoliating pathotype. There were no apparent differences in percentages of open bolls between diseased and symptomless plants for the rest of the plots infested by the defoliating pathotype. Furthermore, in plots with a high inoculum density of the defoliating pathotype the percentage of open bolls was lower in affected plants, which might be due to inadequate maturation of the bolls resulting from reduced nutrient supply.

A numerical relationship between inoculum density of *V. dahliae* and percentage of infected cotton plants at harvest has been demonstrated by several authors (Ashworth *et al*., 1972, 1979). Nevertheless, neither inoculum density nor percentage of infected plants in naturally infested soils appears to be related to yield (Bassett, 1974; Ashworth *et al*., 1979). A power equation showed a high correlation between inoculum density of *V. dahliae* and the ratio of yield in the verticillium wilt-tolerant cultivar Acala GC-510 to that of the susceptible cultivar Acala SJ-2, indicating that yield responses are dependent on disease tolerance in the two cultivars (Paplomatas *et al*., 1992). Percentage of foliar symptoms or defoliation due to verticillium wilt at the end of the season are generally recognized as better indicators of the disease effects on yield than vascular discoloration (Bassett, 1974; Ashworth *et al*., 1979; El-Zik & Yamada, 1981; El-Zik, 1985). These single-point models, relating yield loss to inoculum density or disease intensity level at a specific time, are generally suited to estimate losses caused by short-duration epidemics with a relatively stable apparent infection rate (James, 1974; Teng, 1985). However, for long-duration epidemics with variable infection rates, multiple-point models using levels of the disease intensity at several times or other epidemic characteristics seem more appropriate because they describe better the epidemic development (Burleigh *et al*., 1972; James *et al*., 1972; Teng *et al*., 1979; Teng, 1985; Teng & Bissonnette, 1985). Our results show a significant nonlinear relationship between cotton yield (expressed as the total number of bolls, number of open bolls, or seed cotton yield), the physiological time to appearance of foliar symptoms, and descriptive parameters of D_I increase over time. The best fits of the multiple regression equations studied were obtained when the disease progress curves were represented by the rate of D_I increase over physiological time from sowing instead of the AUDPC. A similar model was developed for stem rust in spring wheat, where yield loss was estimated as a function of the slope of the epidemic line and the growth stage of the host at time of epidemic onset (Calpouzos *et al*., 1976). This type of model, represented by response surface, provides a conceptual framework based on a knowledge of epidemiology and physiology for modelling disease-loss systems (Teng & Gaunt, 1981). Our model does not incorporate the influence of variables such as plant stand, weather, soil type, plant compensation and others, and cannot be used to make accurate predictions in different situations. However, it could be applied to predict the impact of verticillium wilt on yield for specific locations and conditions, using the rate of D_I increase estimated from two or more early disease assessments. Also this model allows for a better understanding of the interactions of cotton plants and *V. dahliae*, by accounting for the effect of different epidemics on yield at different crop growth stages.

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