Inoculum Densities of *Fusarium oxysporum* f. sp. *vasinfectum* and *Meloidogyne incognita* in Relation to the Development of Fusarium Wilt and the Phenology of Cotton Plants (*Gossypium hirsutum*)

J. E. DeVay, A. P. Gutierrez, G. S. Pullman, R. J. Wakeman, R. H. Garber, D. P. Jeffers, S. N. Smith, P. B. Goodell, and P. A. Roberts

First, third, fourth, sixth, and seventh authors: Department of Plant Pathology, University of California, Davis 95616; second author: Department of Environmental Sciences Policy and Management, University of California, Berkeley 94706; fifth author: USDA Cotton Research Station, Shafter, CA 93263, eighth author: CE-DANR, University of California, Parlier 93648, ninth author: Department of Nematology, University of California, Riverside 92521.

Accepted for publication 26 November 1996.

ABSTRACT

DeVay, J. E., Gutierrez, A. P., Pullman, G. S., Wakeman, R. J., Garber, R. H., Jeffers, D. P., Smith, S. N., Goodell, P. B., and Roberts, P. A. 1997. Inoculum densities of *Fusarium oxysporum* f. sp. *vasinfectum* and *Meloidogyne incognita* in relation to the development of Fusarium wilt and the phenology of cotton plants (*Gossypium hirsutum*). *Phytopathology* 87:341-346.

Development of Fusarium wilt in upland cotton (*Gossypium hirsutum*) usually requires infections of plants by both *Meloidogyne incognita* and *Fusarium oxysporum* f. sp. *vasinfectum*. In this study, the soil densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* and the incidence of Fusarium wilt in three field sites were determined in 1982–1984. Multiple regression analysis of percent incidence of Fusarium wilt symptoms on population densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* yielded a significant fit ($R^2 = 0.64$) only on *F. oxysporum* f. sp. *vasinfectum*. Significant *t*-values for slope were also obtained for the interaction of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum*, but densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* were also related on a log₁₀

scale. The physiological time of appearance of first foliar symptoms of Fusarium wilt, based on a degree-days threshold of 11.9°C (53.5°F), was used as a basis for determining disease progress curves and the phenology of cotton plant growth and development. Effects of Fusarium wilt on plant height and boll set were determined in three successive years. Increases in both of these plant characteristics decreased or stopped before foliar symptoms were apparent. Seed cotton yields of plant cohorts that developed foliar wilt symptoms early in the season (before 2,000 F degree-days) were variable but not much different in these years. This contrasted with cohorts of plants that first showed foliar symptoms late in the season (after 2,400 F degree-days) and cohorts of plants that showed no foliar symptoms of wilt. Regression analyses for 1982–1984 indicated moderate to weak correlations ($r = 0.16$ – 0.74) of the time of appearance of the first foliar symptoms and seed cotton yields.

Additional keywords: induced plant disease susceptibility, population densities of *Meloidogyne incognita* and *Fusarium oxysporum* f. sp. *vasinfectum*, root-knot, soil solarization.

Fusarium wilt is a major problem in most cotton-growing regions of the world (4,18). In 1995, it caused an estimated loss of 73,748 bales (217.7 kg/bale) in potential lint yield in the cotton belt of the United States (3). Since the recognition of Fusarium wilt of cotton in Alabama by Atkinson in 1892 (1), the disease has spread and increased in importance, especially in the southeastern United States (18). Fusarium wilt was first found in the San Joaquin Valley of California in 1960 (8). By 1967, it was still confined to about 2 ha; however, by 1983, our surveys indicated that it had spread to over 2,000 ha, involving more than 50 cotton fields in the San Joaquin Valley. The pathogen also has the potential to spread to an additional 122,000 ha of cotton production land with light or sandy soils, which are conducive to the development of Fusarium wilt (5).

Six races of *Fusarium oxysporum* Schlechtend.:Fr. f. sp. *vasinfectum* (Atk.) W. C. Snyder & H. N. Hans. have been recognized, but only race 1 is widely prevalent in the United States (4,18). Race 2 has been found in South Carolina (18).

Soilborne propagules of *F. oxysporum* f. sp. *vasinfectum* consist mainly of chlamydospores in plant debris, and field infestations

have long durations (18). Gin trash and other plant debris as well as cotton seed from fields with Fusarium wilt are also sources of *F. oxysporum* f. sp. *vasinfectum* inoculum (12).

The root-knot nematode, *Meloidogyne incognita*, is associated with *F. oxysporum* f. sp. *vasinfectum* in the development of Fusarium wilt in some cultivars of *Gossypium hirsutum* (18). Two of the four host races of *M. incognita*, race 3 and race 4, parasitize cotton, and to date only race 3 of *M. incognita* has been found attacking cotton in the San Joaquin Valley. Root infections by *M. incognita* increase the colonization of cotton plants by *F. oxysporum* f. sp. *vasinfectum* and their susceptibility to Fusarium wilt (7). It is well known that control of root-knot nematodes results in a marked reduction in the incidence and severity of Fusarium wilt of cotton (13,19). The importance of interactions between *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* in the development of wilt diseases has been extensively studied (13); however, the anatomical and chemical responses of cotton and the overall mechanism of interactions between *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* which influence wilt development are not fully understood (13). Resistance in cotton plants to *M. incognita* is genetically distinct from resistance to *F. oxysporum* f. sp. *vasinfectum* (7,17). Thus, cotton cultivars may or may not have resistance to either or both *M. incognita* and *F. oxysporum* f. sp. *vasinfectum*.

Previous studies have shown that root infection of cotton seedlings by *F. oxysporum* f. sp. *vasinfectum* is favored by low soil

Corresponding author: J. E. DeVay; Fax: 916/752-5674

Publication no. P-1997-0121-04R

This article is in the public domain and not copyrightable. It may be freely reprinted with customary crediting of the source. The American Phytopathological Society, 1997.

temperatures (6) of about 15°C, although increasing air temperatures later in the season are more conducive to foliar wilt development. This result was also apparent in a date-of-planting study (10,11) in which early plantings of cotton cultivar Acala SJ-2 were more severely affected by *Fusarium* wilt than later plantings with *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* at similar inoculum densities. Although root infection by *M. incognita* is a critical factor in wilt development and is sensitive to soil temperature (12), changes in activities of *M. incognita* based on slight changes in soil temperatures at root depth were not apparent (10,11). It appears that other factors which affect plant development, such as high air temperatures and day length, also affect susceptibility to *Fusarium* wilt (4,6).

The objectives of this study were to evaluate the growth and development of cotton plants in fields infested with *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* at different inoculum densities and to determine the predictive value of symptom expression for cotton growth and yield.

MATERIALS AND METHODS

Experimental design. Data were collected each year during 1982–1984 from three experimental field locations, designated A, B, and C, at Shafter, California. The soil type was a Wasco sandy loam (77% sand, 11% silt, and 12% clay), slightly alkaline, and naturally infested with *M. incognita* and *F. oxysporum* f. sp. *vasinfectum*. In Field A, rows of cotton (cultivar Acala SJ-2) were 46 m long on 1-m centers, with two rows for each of five replications. In Fields B and C, rows of cotton were 15.3 m long on 1-m centers, with four rows for each of three replications. In all fields, data were collected on the final incidence of *Fusarium* wilt and on soil densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum*. The phenology of cotton plant growth and development in relation to *Fusarium* wilt was determined only in Field A.

In an additional experimental area in Field A, data were collected in two successive years to compare the time of appearance of foliar symptoms and the discoloration of the vascular tissue in cotton stems at the fourth or fifth internode. The incidence of *Fusarium* wilt in this field area prior to this experiment approached 100%. Before foliar symptoms of *Fusarium* wilt were evident, 10 plants were randomly chosen and tagged each week over 15 weeks to determine the time of appearance of vascular discoloration and foliar symptoms.

Fallowing and solarization of Fields B and C. The purpose of the treatments in Fields B and C was to obtain plots with different population densities of *F. oxysporum* f. sp. *vasinfectum* and *M. incognita*. Field B was fallowed from June 1982 until cotton-planting time the following spring, whereas Field C was solarized.

TABLE 1. Incidence of *Fusarium* wilt of cotton and changes in population densities of *Fusarium oxysporum* f. sp. *vasinfectum* and *Meloidogyne incognita* following soil solarization

Year and treatment	<i>M. incognita</i> (J2/250 cm ³ of soil) ^a	<i>F. oxysporum</i> f. sp. <i>vasinfectum</i> (CFU/g of soil)	Incidence of <i>Fusarium</i> wilt (%)
1982			
Field A	60	2,608	93
Field B (fallowed)	8	1,122	...
Field C (solarized)	0	0.2	...
1983			
Field A	50	2,120	78
Field B (fallowed)	38	765	12
Field C (solarized)	8	7	7
1984			
Field A	107	1,100	95
Field B (fallowed)	163	913	61
Field C (solarized)	15	250	23

^a J2 = number of second-stage juveniles of *Meloidogyne incognita*.

^b Not determined.

The solarized plots were covered with transparent polyethylene sheets (25 µm thick). The soil was then irrigated under the plastic sheets to wet the upper 60 cm, left to solarize for 7 weeks (June 23 to August 13, 1982), and then fallowed until the following spring. The fallowed plots were hand-cultivated to control weeds. Soil temperatures were monitored during the solarization period by thermocouples buried at 15-, 30-, and 45-cm depths. When the plastic sheeting was removed after solarization in August 1982, soil samples were collected from both Fields B and C and analyzed for propagule densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* as described below. The following spring, cotton was planted in rows 15.3 m long on 1-m centers, with four rows for each of three replications.

Soil assays for *M. incognita*. Initial population densities of *M. incognita* were determined by collecting soil samples at planting (April 1982) or shortly thereafter. Soil cores were collected with an Oakfield tube (2.5 cm in diameter) from the upper 30 cm of soil. Duplicate samples were collected and analyzed for each replication, each sample consisting of 12 cores of soil randomly collected from midrow locations. Second-stage juveniles (J2) of *M. incognita* were extracted from a 250-cm³ subsample of soil by the wet sieving–Baermann funnel mist extraction method (16). The numbers reported represent absolute counts per 250 cm³ of soil.

Soil assays for *F. oxysporum* f. sp. *vasinfectum*. In April, or shortly after planting, population densities of *F. oxysporum* f. sp. *vasinfectum* and other *Fusarium* species in Field A were determined from six midrow soil collections, each of which consisted of 12 randomly chosen soil cores from depths of 0 to 30 cm. The soil samples were combined and mixed to represent the six midrow collections and then air-dried for 2 weeks at 22 to 24°C. Duplicate 5-g subsamples were diluted in 0.1% water agar, and 1-ml aliquots from five dilutions, ranging from 1:100 to 1:500, were plated on peptone-PCNB (*p*-chloronitrobenzene) agar medium (14).

Soil sampling and plating procedures for *Fusarium* species in Fields B and C were similar to those used for Field A, except that five composite soil samples were collected from soil depths of 0 to 30 cm. In addition to *F. oxysporum* f. sp. *vasinfectum*, colonies of other *Fusarium* species in Fields A, B, and C were identified.

Fig. 1. Disease progress curves in Field A. The percent incidence of *Fusarium* wilt was recorded weekly and plotted as a function of physiological time after planting, above a threshold of 11.9°C (53.5°F), based on the appearance of first foliar symptoms in 1982, 1983, and 1984. Population densities of *Meloidogyne incognita* (MI) are reported as the number of second-stage juveniles per 250 cm³ of soil. Population densities of *Fusarium oxysporum* f. sp. *vasinfectum* (FOV) are reported as CFU per gram of soil.

After incubation of the agar dilution plates for 6 days at 22 to 24°C, colonies resembling *F. oxysporum* f. sp. *vasinfectum* in colony type were transferred from each soil sample to potato-dextrose agar to prepare inoculum for pathogenicity tests. The bottom third of the taproots of 1-week-old cotton seedlings (cultivar Acala SJ-2) were excised, and the remaining roots were immersed for 3 min in a suspension of conidia (3.5×10^5 /ml) collected from the colonies on potato-dextrose agar. The inoculated seedlings were then planted in UC soil mix (2). The plants were placed in a greenhouse at 27 to 32°C (day temperature) and after 2 to 3 weeks were rated for foliar and vascular symptoms of Fusarium wilt. A known isolate of *F. oxysporum* f. sp. *vasinfectum* was used as a control treatment for comparison with the unknown isolates. The hypocotyl of each seedling was cut transversely to determine the presence or absence of vascular browning. The density of *F. oxysporum* f. sp. *vasinfectum* propagules per gram of soil was calculated from the colony frequency in dilution plates and the number of pathogenic isolates present among approximately 4,500 isolates tested.

Cotton phenology and disease development. The influence of Fusarium wilt on the phenology and development of cotton plants was determined in Field A, with five new cohorts of 10 plants chosen each week for 15 weeks. Plants in each cohort were tagged to record when they first showed foliar wilt symptoms. Each cohort was measured weekly for plant height, boll set, and seed cotton yields in three successive years. Included each week were cohorts of plants with no foliar symptoms of Fusarium wilt. As the growing season progressed each year, the plants were carefully monitored without destructive sampling. Plant densities ranged from 12 to 15 plants per meter of row.

Disease progress curves. The development and incidence of Fusarium wilt were observed in three successive years in Field A. Counts of diseased plants were recorded on a cumulative weekly basis and plotted as a function of physiological time elapsed after planting, above a threshold of 53.5°F (11.9°C) (9,20). The experimental plot used for this study in Field A was adjacent to the one used for the phenology study described above and included a different population of plants.

Data analysis. Linear and nonlinear regression of seed cotton yields on physiological time after planting were made. Multiple linear regressions of the percent incidence of Fusarium wilt on population densities *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* were also made. Only the slopes yielding significant *t*-values were kept in the step-down regression.

RESULTS

Disease progress. In the presence of high population densities of both *M. incognita* and *F. oxysporum* f. sp. *vasinfectum*, the rate of increase of Fusarium wilt in cultivar Acala SJ-2 in Field A was variable. Each year, 78 to 95% of the plants showed foliar symptoms by the end of the season (Table 1 and Fig. 1).

TABLE 2. Population densities of *Fusarium* species in Fields A, B, and C in 1982

<i>Fusarium</i> species	Population density (CFU/g of soil) ^a		
	Field A	Field B	Field C
Total <i>Fusarium</i> species	5,238	2,871	7
<i>F. oxysporum</i> f. sp. <i>vasinfectum</i>	2,608	1,122	0.2
<i>F. oxysporum</i> (saprophytic)	335	435	0
<i>F. roseum</i>	625	711	2
<i>F. solani</i>	911	551	5
<i>F. episphaeria</i>	759	52	0

^a Values for Field A are averages of six composite soil samples or replications, whereas values for Fields B and C are averages of five composite soil samples, all from soil depths of 0 to 30 cm.

Effects of fallowing and soil solarization. Population densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* in Field B (fallowed) and Field C (solarized) over the 3-year study are shown in Table 1. During solarization in 1982, the average maximum soil temperature was 47 to 48°C at a depth of 15 cm, while in fallowed soil the average maximum temperature was 36°C. In solarized soil (Field C), population densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* were undetectable. In fallowed soil

Fig. 2. Influence of Fusarium wilt on cotton plant height in physiological time after planting during 1982–1984. The first data point in each graph represents the time when foliar symptoms first appeared.

(Field B), population densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* were detected but were less than in Field A. However, in 1983 and 1984, as the population densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* began to increase in Fields B and C, the incidence of Fusarium wilt also increased (Table 1).

Effect of population densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* on the incidence of Fusarium wilt.

Fig. 3. Effect of Fusarium wilt on boll set in physiological time after planting in 1982-1984. The first data point in each graph represents the time when foliar symptoms first appeared.

These analyses are based on the population densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* in soil and on the percent incidence of Fusarium wilt symptoms in all fields and all years combined (Table 1). Multiple regression analysis of percent incidence of Fusarium wilt symptoms on the population density of *M. incognita* (MI) and the population density of *F. oxysporum* f. sp. *vasinfectum* (FOV) yielded a significant fit only on the latter:

$$\text{Percent incidence of Fusarium wilt symptoms} = 16.86 + 0.032 \text{ FOV} \quad df = 6, \quad F = 8.98, \quad R^2 = 0.64$$

Fig. 4. Seed cotton yields of cohorts of plants plotted as a function of the physiological time of appearance of first foliar symptoms during 1982-1984. Each data point represents a cohort of 10 plants.

Significant *t*-values for slope were also obtained for the interaction of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum*:

$$\begin{aligned} \text{Percent incidence of Fusarium wilt symptoms} \\ = 12.12 + 0.00052(\text{FOV} * \text{MI}) \\ \text{df} = 6, \quad F = 20.40, \quad R^2 = 0.803 \end{aligned}$$

However, an examination of the data in Table 1 shows that the population density of *M. incognita* in 1984 (163 J2/250 cm³ of soil) is large compared to other values for *M. incognita*. With this value removed, the regression equation was

$$\begin{aligned} \text{Percent incidence of Fusarium wilt symptoms} \\ = 189.30 + 2.66 \text{ MI} + 0.030 \text{ FOV} - 267.75 \log_{10} \text{MI} \\ + 40.40 \log_{10} \text{FOV} \quad \text{df} = 5, \quad F = 48.22, \quad R^2 = 0.99 \end{aligned}$$

$$\log_{10} \text{MI} = 0.52 + 0.378 \log_{10} \text{FOV}, \quad \text{hence}$$

$$\text{MI} = 3.33 \text{ FOV}^{0.378} \quad \text{df} = 5, \quad F = 12.86, \quad R^2 = 0.87$$

This analysis indicates that on a log scale population densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* are strongly correlated with each other and with the development of Fusarium wilt.

Population densities of *Fusarium* species. In addition to *F. oxysporum* f. sp. *vasinfectum*, saprophytic *F. oxysporum*, *F. solani*, *F. episphaeria*, and *F. roseum* were the main species detected in Fields A, B, and C in 1982 (Table 2).

Effects of Fusarium wilt on plant height. Weekly measurements of plant height based on cumulative degree-days for the three growing seasons are shown in Figure 2. In each cohort, the appearance of the first foliar symptoms was associated with a rapid slowing and eventual cessation of growth. The height of plants with early symptoms of Fusarium wilt was less than that of plants without foliar symptoms or plants that developed foliar symptoms late in the growing season. Stem growth in most cohorts of plants was slowed before foliar symptoms were apparent.

Effect of Fusarium wilt on boll set. Plants that were symptomatic early in the growing season set and ripened few or no bolls. Plants showing foliar wilt symptoms progressively later in the season were also stunted and set fewer bolls than healthy plants (Fig. 3). However, once set, bolls were seldom shed and continued to mature and eventually opened.

Effects of Fusarium wilt on seed cotton yields. In the cohorts of plants that developed foliar symptoms of Fusarium wilt before 2,000 F degree-days (1,110 C degree-days) each year, seed cotton yields were more variable but on average not much different from those of plants that first developed foliar symptoms after 2,400 F degree-days (1,332 C degree-days) (Fig. 4). Regression analyses for 1982 ($r = 0.74$; $\text{prob} > F = 0.0015$; intercept = 26.7), 1983 ($r = 0.69$; $\text{prob} > F = 0.0057$; intercept = 2.95), and 1984 ($r = 0.16$; $\text{prob} > F = 0.570$) indicated decreasing correlations between the time of foliar symptom development and seed cotton yields over the 3-year period. Vascular browning of cotton stems was a consistent indicator of infection of cotton by *F. oxysporum* f. sp. *vasinfectum*. For example, in the Fusarium wilt plots in 1984, vascular browning preceded foliar symptoms by at least 300 F degree-days (167 C degree-days) (Fig. 5). Similar results were recorded in 1983 (data not shown). Seed cotton yields of plants showing no foliar symptoms of Fusarium wilt were significantly greater than those of plants with foliar symptoms (Fig. 4).

DISCUSSION

This study was mainly concerned with the effects of population densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* on the growth and development of cotton plants affected by Fusarium wilt and the overall effect on yields of seed cotton. During the growing season, cohorts of both healthy and diseased plants were tagged each week and analyzed for changes in height, numbers of bolls, and finally seed cotton yields. Disease progress curves dur-

ing the 3 years of this research reached end-of-season incidences of Fusarium wilt in 78 to 95% of the plants (Fig. 1 and Table 1), with variations between the curves in the rate of disease development. The development and incidence of foliar symptoms of Fusarium wilt are temperature-sensitive and are greatest during periods of high temperatures, approximately 28°C or higher (4). Thus, the differences between the disease progress curves in Figure 1 may reflect variations in seasonal temperatures as well as differences in population densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum*.

Infection of plants by both *M. incognita* and *F. oxysporum* f. sp. *vasinfectum* is necessary for full expression of Fusarium wilt (7,18), but the basis of the interaction, including environmental effects such as temperature, is poorly defined (13). However, in a date-of-planting study with little variability in inoculum densities of *M. incognita* and *F. oxysporum* f. sp. *vasinfectum*, marked differences in the severity and incidence of Fusarium wilt occurred (11). Moreover, Jeffers (10) analyzed root exudations of cotton plants infected by *M. incognita* and *F. oxysporum* f. sp. *vasinfectum*, and although differences in concentrations of sugars, amino acids, and other metabolites were found, there were no consistent differences that characterized infected and healthy plants.

The incidence of vascular browning, a consistent indicator of plant infection by *F. oxysporum* f. sp. *vasinfectum*, may approach 100% of plants by 800 degree-days, and foliar symptoms usually develop in these plants (Fig. 5). Unlike vascular browning due to Verticillium wilt, which has little effect on plant phenology and yield of seed cotton, vascular browning due to Fusarium wilt is correlated with plant growth and yields of seed cotton before foliar symptoms appear. In Verticillium wilt, infection of plant roots and disease development are progressive throughout the growing season (15), but in Fusarium wilt an early cycle of infection appears sufficient to induce slow growth and reductions in seed cotton yields in plant populations for the remainder of the growing season.

Fig. 5. Percent incidence of vascular browning and foliar symptoms in plants affected by Fusarium wilt in 1984, recorded weekly and plotted as a function of physiological time and. The first data point in each graph represents the time when symptoms first appeared.

By the time foliar symptoms of *Fusarium* wilt appeared, the growth and development of cotton plants had already begun to slow down or cease (Figs. 2 and 3). Low seed cotton yields reflect the early effect of *Fusarium* wilt. However, plants not showing foliar symptoms and viewed as healthy yielded approximately four times as much seed cotton as plants with foliar symptoms (Fig. 4).

The number of main stem nodes is a linear function of physiological time until photosynthate stress begins, a stage when most of the photosynthate production is allocated to rapidly growing fruits (9,20). However, the development of vascular discoloration and foliar symptoms of *Fusarium* wilt is closely associated with decreases in node and internode development, as evidenced by stunting and arrested growth of infected plants (5).

Early efforts to control or manage *Fusarium* wilt consisted of soil fumigation to reduce the population density of *M. incognita*. However, with increasing constraints on the use of soil fumigants, recent research on the selection and development of cotton cultivars tolerant or resistant to *M. incognita*, *F. oxysporum* f. sp. *vasinfectum*, or both has yielded several outstanding cultivars, such as Acala Prema and Acala Nem-X (7).

ACKNOWLEDGMENTS

Financial support for this research was provided by the Consortium of Pest Management, Texas A&M University, College Station, and the U.S. Environmental Protection Agency, Grant L800151.

LITERATURE CITED

1. Atkinson, G. F. 1892. Some diseases of cotton. III. Frenching. Ala. Agric. Exp. Stn. Bull. 41:19-29.
2. Baker, K. F., ed. 1957. The UC System for Producing Healthy Container-Grown Plants. University of California, Division of Agricultural Sciences, Berkeley.
3. Blasingame, D. 1996. Cotton disease loss estimate committee report. Page 227 in: 1996 Proc. Beltwide Cotton Conf. P. Dugger and D. A. Richter, eds. National Cotton Council of America, Memphis, TN.
4. DeVay, J. E. 1986. Half a century dynamics and control of cotton diseases: *Fusarium* and *Verticillium* wilts. Pages 35-41 in: 1986 Proc. Beltwide Cotton Conf. J. Brown, ed. National Cotton Council of America, Memphis, TN.
5. DeVay, J. E., Garber, R. H., Pullman, G. S., Smith, S. N., and Goodell, P.

1983. Epidemiological studies on *Fusarium* wilt of cotton. Page 17 in: 1983 Proc. Beltwide Cotton Conf. J. Brown, ed. National Cotton Council of America, Memphis, TN.
6. Ebbels, D. L. 1975. *Fusarium* wilt of cotton: A review with special reference to Tanzania. Cotton Grow. Rev. 52:295-339.
7. Garber, R. H., Jorgenson, E. C., Smith, S. N., and Hyer, A. H. 1979. Interaction of population levels of *Fusarium oxysporum* f. sp. *vasinfectum* and *Meloidogyne incognita* on cotton. J. Nematol. 11:133-137.
8. Garber, R. H., and Paxman, G. A. 1963. *Fusarium* wilt of cotton in California. Plant Dis. Rep. 47:398-400.
9. Gutierrez, A. P., DeVay, J. E., Pullman, G. S., and Friebehtshauser, G. E. 1983. A model of *Verticillium* wilt in relation to cotton growth and development. Phytopathology 73:89-95.
10. Jeffers, D. P. 1991. Interaction of soil temperature, cotton genotype and *Meloidogyne incognita* infection on the susceptibility of *Gossypium hirsutum* to *Fusarium oxysporum* f. sp. *vasinfectum* infection and *Fusarium* wilt development. Ph.D. thesis, University of California, Davis.
11. Jeffers, D. P., and Roberts, P. A. 1993. Effect of planting date and host genotype on the root-knot nematode-*Fusarium* wilt disease complex of cotton. Phytopathology 83:645-654.
12. Jeffers, D. P., Smith, S. N., Garber, R. H., and DeVay, J. E. 1984. The potential spread of the cotton *Fusarium* wilt pathogen in gin trash and planting seed. (Abstr.) Phytopathology 74:1139.
13. Mai, W. F., and Abawi, G. S. 1987. Interactions among root-knot nematodes and *Fusarium* wilt fungi on host plants. Annu. Rev. Phytopathol. 25:317-338.
14. Nash, S. N., and Snyder, W. C. 1962. Quantitative estimation by plate counts of propagules of the bean root rot *Fusarium* in field soils. Phytopathology 52:567-572.
15. Pullman, G. S., and DeVay, J. E. 1982. Epidemiology of *Verticillium* wilt of cotton: Effects of disease development on plant phenology and lint yield. Phytopathology 72:554-559.
16. Roberts, P. A. 1987. Influence of planting date of carrot on *Meloidogyne incognita*. Nematologica 33:335-342.
17. Shepherd, R. L. 1986. Cotton resistance to the root knot-*Fusarium* wilt complex. II. Relation to root-knot resistance and its implications on breeding for resistance. Crop Sci. 26:233-237.
18. Smith, S. N., Ebbels, D. L., Garber, R. H., and Kappelman, A. J., Jr. 1981. *Fusarium* wilt of cotton. Pages 29-38 in: *Fusarium: Diseases, Biology, and Taxonomy*. P. E. Nelson, T. A. Toussoun, and R. J. Cook, eds. Pennsylvania State University Press, University Park.
19. Starr, J. L., Jeger, M. J., Martyn, R. D., and Schilling, K. 1989. Effects of *Meloidogyne incognita* and *Fusarium oxysporum* f. sp. *vasinfectum* on plant mortality and yield of cotton. Phytopathology 79:640-646.
20. Wang, Y., Gutierrez, A. P., Oster, G., and Daxl, R. 1977. A population model for plant growth and development: Coupling cotton-herbivore interaction. Can. Entomol. 109:1359-1374.