Effect of Meloidogyne incognita acrita on the Susceptibility of Cotton Plants to Verticillium albo-atrum

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ABSTRACT

Addition of 1,000-2,000 *Meloidogyne incognita acrita* larvae/pot at pre-emergence, first-leaf, or third-leaf stages of development of *Gossypium hirsutum* 'Deltapine Smooth Leaf' (DSL) and *G. barbadense* 'Pima S-2' (PS-2), followed 3 days later by 30-120 ml/pot of a suspension of *Verticillium albo-atrum*, significantly increased the number of plants infected by this fungus. The addition of 2,000 larvae/pot at pre-emergence, first-leaf, or third-leaf stages, followed 3, 7, 15, or 27 days later by 60 ml/pot of a suspension of *V. albo-atrum*, increased the susceptibility of all plants to *V. albo-atrum* except for those of DSL inoculated 27 days after the third-leaf stage. Symptoms were more severe on plants inoculated with the fungus and high concentrations of the nematode than on plants inoculated only with the fungus. The susceptibility to *V. albo-atrum* of nematode-treated PS-2 plants equaled or exceeded the susceptibility of DSL plants of comparable ages. The number of galls induced on cotton roots by the nematode was not influenced by *V. albo-atrum*. Potassium hydroxide-soluble carbohydrates (CHO) in roots of both cultivars and susceptibility of the plants to *V. albo-atrum* increased as the seedlings aged through approximately the first- to third-leaf stages. *M. incognita acrita* had no significant effect on CHO levels in the roots of either cotton cultivar.

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Additional key words: breeding, carbohydrates, control, galls, inoculum potential.

Root-lesion nematodes (*Pratylenchus penetrans*) are known to increase the incidence of Verticillium wilt in eggplants (*Solanum melongena*) (15, 19), peppermint (*Mentha piperita*) (4, 8), potatoes (*Solanum tuberosum*) (17), strawberries (*Fragaria vesca*) (1), and tomatoes (*Lycopersicon esculentum*) (18). Comparable investigations with cotton plants have mainly involved the root-knot nematode *Meloidogyne incognita acrita* Chitwood. Cauquil & Shepherd (5) found that this nematode acted synergistically with several fungi to increase the severity of cotton seedling diseases. Other reports (3, 16) suggest that *M. incognita acrita* might be associated with increasing incidence and severity of Verticillium wilt; however, McClellan et al. (14) could not reduce the incidence of Verticillium wilt by preplant applications of ethylene dibromide to soil also infested with *M. incognita acrita*.

Several authors (26, 28, 29) have suggested that increased carbohydrate (CHO) levels in roots may be associated with increased susceptibility of the plants to *V. albo-atrum*. *M. incognita acrita* reduces the CHO level in the galled portions of tomato roots (23), which suggests that infection by this nematode might reduce the susceptibility of cotton plants to *V. albo-atrum*.

Generally, the short staple, Upland cotton species *Gossypium hirsutum* L. has been considered more susceptible to *V. albo-atrum* than the long staple, Anglo-Egyptian species *G. barbadense* L. (24). We investigated whether infection by *M. incognita acrita* of the Upland cultivar 'Deltapine Smooth Leaf' (DSL) and the Anglo-Egyptian cultivar 'Pima S-2' (PS-2) affected their susceptibility to *V. albo-atrum* or CHO levels in their roots.

MATERIALS AND METHODS.—*General procedures.*—Acid-delinted seeds of DSL and PS-2 were planted in 15-cm pots containing a dry-heat (121 C)-treated soil mixture consisting of loam, sand, and peat moss (1:3:1). Seedlings were thinned to five uniform plants/pot.

Stock cultures of *Meloidogyne incognita acrita* (originating from several egg masses collected from infected cotton plants by E. L. Nigh, Jr.) were maintained upon *L. esculentum* Mill. 'Bonny Best'. To obtain inoculum, we washed several heavily galled tomato roots in tap water, then placed them over a pan and subjected them to intermittent misting. At 24-hr intervals we collected the nematodes by sieving the water that had accumulated in the pan. A suspension of 250 nematodes/ml was used as the basic unit of inoculum.

We infested soil by pouring inoculum into a hole, ca. 8-10 cm deep and centrally located in each pot (12). The hole was subsequently filled with soil and the plants then were irrigated.

The methods for growing, inoculating, and reisolating *V. albo-atrum* have been described (12). The least significant differences (LSDs) given in the tables should be used for both horizontal and vertical comparisons of appropriate data. These were derived either from multiple factorial analyses of pooled data resulting from the various treatments in a given experiment (12) or from an appropriate analysis of variance. Noninoculated plants and plants inoculated singly with *M. incognita acrita* or *V. albo-atrum* were included in all tests. Experiments were terminated 28 days after the Verticillium inoculations.

Inoculations of variously aged plants.—Acid-delinted seeds were planted on a schedule that provided on a given date plants that either had just emerged or were in the first- or third-leaf stages. Three days prior to the given date, soil in five groups of 16 pots for each stage of each cultivar was infested with either 0, 250, 500, 1,000, or 2,000 nematode larvae/pot. Three days after application of these treatments 0, 30, 60, or 120 ml of *V. albo-atrum* suspension were added to the soil in each of four replicate pots for each nematode concentration tested. An additional level of 4,000 nematodes/pot was tested in a second trial of the experiment. Since the results of the second trial confirmed those of the first trial (11), only the details of the first experiment are presented here.

Spaced inoculations of nematodes and Verticillium.—About 3 days before DSL and PS-2 plants reached emergence, first-leaf, and third-leaf stages, 2,000 nematode larvae were added to each of 47 pots for each growth stage of each cultivar. Three, 7, 15, or 27 days later, 60 ml of the *V. albo-atrum* suspension also were added to each of four replicate pots for each growth stage and each cultivar. When each of the latter three Verticillium inoculations were made, plants in a second lot of five pots for each growth stage and cultivar were collected for gall counts and CHO analyses. The remainder of the plants representing each growth stage and cultivar were used as nematode-inoculated controls. Comparable numbers of plants were inoculated only with *V. albo-atrum* or left noninoculated. The test was not repeated.

Gall counts.—At the conclusion of the first experiment on the relation of susceptibility to plant age, roots were removed from one plant exhibiting vascular discoloration and from one without vascular discoloration (if present) from each pot. The roots were washed in tap water, boiled for 1 min in acid fuchsin-lactophenol (13), then destained in lactophenol (2). For the spaced inoculation experiment, gall numbers were determined when the plants were inoculated with *V. albo-atrum*. Galls were counted on the roots of one plant from each of five pots of each series. Washed roots were stained for 4 hr in a solution consisting of equal volumes of glacial acetic acid and 95% ethanol (containing 0.175 mg acid fuchsin/ml) (7), cleared in saturated aqueous chloral hydrate, then mounted in lactophenol. Galls were counted by means of a dissecting microscope at X20 magnification (7).

CHO determinations.—Roots of 20 nematode-inoculated plants harvested from each of the treatments involved in the spaced inoculation test were bulked; three subsamples then were analyzed by the anthrone procedure (12, 29) for potassium hydroxide-extractible CHO concentrations. Comparable noninoculated plants were used as controls.

RESULTS.—*Effect of M. incognita acrita on the susceptibility of cotton plants of various ages to V. albo-atrum.*—The susceptibility of the plants to *V. albo-atrum* alone increased as the age of the plants increased. The disease incidence also increased as the volume of inoculum was increased (Table 1). Addition of 250 or 500 nematodes/pot did not significantly alter the susceptibility of any plants inoculated with *V. albo-atrum* except for the combination of 500 nematodes plus 120 ml of the fungus. However, at levels of 1,000 and 2,000 nematodes/pot, the susceptibility of the plants to *V. albo-atrum* was significantly increased for all levels of fungal inoculum tested (Table 1).

Susceptibility to *V. albo-atrum* of plants at

TABLE 1. Infection by *Verticillium albo-atrum* of the cotton cultivars Deltapine Smooth Leaf (DSL) and Pima S-2 (PS-2) concurrently inoculated with *Meloidogyne incognita acrita*[a]

Inoculum level (Nematodes/ 15-cm pot)	Mean percentage infection by *V. albo-atrum*								
	Cultivars inoculated[b]		Growth stage when inoculated[c]			*V. albo-atrum* suspension ml/pot[d]			
	DSL	PS-2	Emergence[e]	First-leaf	Third-leaf	0	30	60	120
0	26.7	25.0	10.6	32.5	34.4	0.0	27.5	35.0	40.8
250	26.3	27.1	11.9	33.8	34.4	0.0	28.3	26.7	41.7
500	26.3	29.6	12.5	36.3	35.0	0.0	28.3	36.7	46.7
1,000	28.8	37.1	13.1	40.0	45.0	0.0	36.7	42.5	52.5
2,000	31.3	44.6	18.1	45.6	50.0	0.0	40.8	50.0	60.8

[a] Plants were inoculated with *M. incognita acrita* 4 days before reaching the indicated age; and with *V. albo-atrum*, 3 days after inoculation with the nematodes; readings for vascular discoloration and isolations were made 28 days later; treatments, each with five plants, were replicated 4 times. Multiple factorial analyses of the indicated relationships were made on pooled data.

[b] Each value is the mean for 48 sets of plants (three ages X four Verticillium inoculum concentrations X four replications); LSD at 5% = 3.9.

[c] Each value is the mean for 32 sets of plants (two cultivars X four Verticillium inoculum concentrations X four replications); LSD at 5% = 4.8.

[d] Each value is the mean for 24 sets of plants (two cultivars X three ages X four replications); LSD at 5% = 5.5.

[e] At 6 days after planting.

different stages of growth increased as the numbers of *M. incognita acrita* were increased. The increases were significant for plants at the emergence stage and inoculated with 2,000 nematodes/pot, and for first- and third-leaf stage plants inoculated with 1,000 or more nematodes/pot. The third-leaf stage was significantly more susceptible than the first-leaf stage at the level of 1,000 nematodes/pot. The emergence stage was significantly less susceptible than the other two stages regardless of nematode concentrations (Table 1).

The susceptibility of DSL to *V. albo-atrum* was significantly increased over that of control plants with the addition of 2,000 nematodes/pot. However, the susceptibility of PS-2 was significantly increased with the addition of 500 or more nematodes/pot. PS-2 also was significantly more susceptible than DSL when each was treated with 1,000 or 2,000 nematodes/pot (Table 1).

The mean percentage infection (MPI) of DSL and PS-2 by *V. albo-atrum* following exposures of the plants to the various nematode and *V. albo-atrum* inocula were, respectively, 11.8 and 14.8 for emerging plants; 34.5 and 40.8 for first-leaf stage plants; and 37.3 and 42.5 for third-leaf stage plants (LSD at 5% = 3.0 for all relationships). When data relating to plant ages and amounts of nematode inocula were pooled, the MPI of DSL and PS-2 by *V. albo-atrum*, were, respectively, 32.3 and 32.3 for treatments involving 30 ml/pot of *V. albo-atrum*; 36.4 and 44.3 for 60 ml/pot; and 43.0 and 54.0 for 120 ml/pot (LSD at 5% = 3.5 for all relationships).

The addition of 4,000 nematodes/pot in a second trial (11) in all cases resulted in further increases in the susceptibility of the plants to *V. albo-atrum*; in 75% of these instances, the increases were significantly greater than those observed for the treatments with 2,000 nematodes/pot. Earlier and more severe defoliation was noted on plants inoculated with both *V. albo-atrum* and high concentrations of the nematode (1,000-4,000 larvae/pot) than on those inoculated only with the fungus; the degree of defoliation was more severe on DSL than on PS-2 plants.

Effect of the time interval between nematode and Verticillium inoculations on the susceptibility of cotton plants to V. albo-atrum.—In the absence of the nematode, both cultivars increased in susceptibility to *V. albo-atrum* until they reached the third- to fourth-leaf stage; susceptibility decreased after the fifth- to sixth-leaf stage (Table 2). The two cultivars did not differ significantly in the incidence of Verticillium wilt regardless of plant age.

Our adding 2,000 nematodes/pot at the pre-emergence, early first-, and early third-leaf stages, followed 3, 7, 15, or 27 days later by our infesting the soil with *V. albo-atrum*, significantly increased infection by the fungus of all plants of both cultivars, except for DSL plants that were in the bud stage when the fungus was added to the pots (Table 2). The effect of *M. incognita acrita* on the older cotton plants diminished, however, as the interval between treatments with the nematode and with the fungus was increased. In this test, PS-2 plants inoculated

TABLE 2. Infection by *Verticillium albo-atrum* of the cotton cultivars 'Deltapine Smooth Leaf' (DSL) and 'Pima S-2' (PS-2) exposed to *Meloidogyne incognita acrita* (2,000 larvae/15 cm-pot) at intervals after planting and subsequently treated at intervals with *V. albo-atrum*[a] (60 ml/pot)

Growth stage of plant when soil was infested with		Days between introduction of nematodes and fungus	Mean percentage infection by *Verticillium* (VA)[b]			
			DSL		PS-2	
Nematodes	Verticillium		VA	VA + nema	VA	VA + nema
Pre-emergence	Early emergence	3	10.0	35.0	15.0	45.0
	Cotyledon	7	35.0	55.0	40.0	65.0
	One-leaf	15	65.0	85.0	65.0	95.0
	Three-leaf	27	70.0	85.0	70.0	95.0
Early one-leaf	One-leaf	3	60.0	95.0	65.0	100.0
	One-two-leaf	7	65.0	100.0	70.0	100.0
	Three-four-leaf	15	70.0	90.0	75.0	95.0
	Five-six-leaf	27	80.0	90.0	80.0	95.0
Early three-leaf	Three-leaf	3	80.0	100.0	80.0	100.0
	Three-four-leaf	7	90.0	100.0	80.0	100.0
	Five-six-leaf	15	80.0	90.0	75.0	95.0
	DSL:bud, PS-2:seven-eight-leaf	27	60.0	65.0	60.0	70.0

[a] Readings were made 28 days after inoculation with the fungus; treatments, each with five plants, were replicated four times.

[b] LSD at 5% = 9.4. No Verticillium infection occurred in noninoculated plants treated only with nematodes.

TABLE 3. Gall numbers and root carbohydrate (CHO) levels of the cotton cultivars Deltapine Smooth Leaf (DSL) and Pima S-2 (PS-2) exposed at various ages to 2,000 larvae/pot of *Meloidogyne incognita acrita*

Plant growth stage inoculated	Time of harvesting[a]		Galls per plant[b]		CHO mg/g dry root[c]			
					DSL		PS-2	
	Days after nema infestation	Plant growth stage	DSL	PS-2	Control	Nemas	Control	Nemas
Pre-emergence	7	Cotyledon	2	3	62.7	65.3	73.7	72.0
	15	One-leaf	45	64	77.3	80.0	78.7	78.7
	27	Three-leaf	74	75	87.0	83.3	72.0	71.7
Early one-leaf	7	One-two-leaf	25	27	81.3	76.7	68.0	68.0
	15	Three-four-leaf	91	84	134.0	134.7	113.3	116.0
	27	Five-six-leaf	103	93	130.0	127.3	140.7	135.7
Early three-leaf	7	Three-four-leaf	29	28	127.3	127.3	104.0	106.0
	15	Five-six-leaf	96	80	114.0	119.3	125.7	124.0
	27	DSL:bud, PS-2:seven-eight-leaf	94	97	174.0	173.0	199.3	205.0

[a] Determinations were made at the time comparable plants were inoculated with *V. albo-atrum* (See Table 2).

[b] Average based on one plant from each of five replicate pots.

[c] Means of three determinations/sample. LSD at 5% = 8.3.

with nematodes at the pre-emergence stage were more susceptible to *V. albo-atrum* than were comparably treated DSL plants (Table 2).

Gall numbers consistently increased as the number of nematodes used as inoculum was increased. In the first experiment, the numbers of galls that developed by 31 days after infestation of the soil ranged from an average of 7-9 to 83-121/plant when soils were infested with 250 and 4,000 nemas/pot, respectively. No consistent differences in gall numbers were noted between plants of various ages, between cultivars, or between Verticillium-infected and noninfected plants. In the second experiment, galls on PS-2 roots consistently increased with time to a maximum average of 97 galls/plant by 27 days after inoculation; similar increases, with one exception, occurred with DSL (Table 3). Plants of both cultivars that were inoculated at the first- and third-leaf stages developed 93-103 galls/plant by 27 days; roots of plants inoculated at the pre-emergence stage developed 74-75 galls/plant in the same interval (Table 3).

Concentrations of root CHO generally increased in healthy PS-2 to the seventh- to eighth-leaf stages. Except for a decrease in concentration at the fifth- to sixth-leaf stages, similar increases occurred with DSL. *M. incognita acrita* had no significant influence on the concentrations of CHO at any growth stage of either cultivar (Table 3).

DISCUSSION.—These data corroborate prior reports (12, 25, 29, 30) that young cotton seedlings are less susceptible to *V. albo-atrum* than older plants. They also confirm the observation (29) that susceptibility declines after the sixth-leaf stage. That PS-2 had the potential for susceptibility to *V. albo-atrum* at least equal to that of DSL also was confirmed (12, 29).

Tylenchorhynchus capitatus and *M. incognita* have recently been reported to increase the incidence and severity of Verticillium wilt of the tomato cultivar 'Floradel' in greenhouse tests (21). Our greenhouse studies show that *M. incognita acrita* also can increase the susceptibility of cotton plants to *V. albo-atrum*, thus substantiating what has been surmised by others (3, 16). The degree of the effect of the nematode was mediated, however, by the concentrations of the nematodes and of *V. albo-atrum*, by the cotton cultivars involved, and by the physiological ages of the treated plants. The greatest effect was on plants, particularly those of PS-2, that were inoculated at the early stages of growth.

Resistance in cotton plants to *V. albo-atrum* may involve in part an inability of the fungus to become secondarily established in areas of the xylem above the initial area of invasion (9). This inability to colonize sites higher in the plant could result from a reduced rate of vessel maturation, which would prevent acropetal movement of conidia (25). We obtained results comparable to those reported for a similar study involving *Rhizoctonia solani* (12). *V. albo-atrum* could be recovered from the hypocotyls of a greater number of plants that had been exposed at the pre-emergence stage to large concentrations of the nematode, than could be recovered from comparable nontreated plants. Although this suggests that *M. incognita acrita* might have influenced the maturation rate of vessels, the fact that the susceptibility of older plants also was increased by nematode treatments indicates that other mechanisms may be involved.

Increases in susceptibility of plants, including cotton, to *V. albo-atrum* might be a function of increases in CHO concentrations in their roots (26, 28, 29). This relationship was demonstrated for DSL plants between approximately the first- and third-leaf stages and extending to the fifth- to sixth-leaf stages for PS-2 plants when neither cultivar was exposed to nematodes. Although infection by *M. incognita acrita* enhanced the susceptibility of these cultivars to *V. albo-atrum*, changes in concentrations of root CHO

from those found in nematode-free roots were not observed. Therefore, other mechanisms that can influence changes in susceptibility must be considered. The lack of an effect of nematode infection on CHO levels does not agree with the report by Owens & Specht (23). That their analyses were made only on galled portions of roots, or that tomatoes respond differently to this nematode may account for our differing results.

Generally, more nematode-treated PS-2 plants became infected with *V. albo-atrum* than did similarly treated DSL plants of the same age. However, these differences could not be explained in terms of the numbers of galls on their roots. The numbers of galls increased as the interval after the exposure of the plants to the nematodes was lengthened. Similarly, when soils were infested with nematodes just prior to plant emergence, the longer the interval before inoculating with *V. albo-atrum* the greater the number of Verticillium-infected plants. Although nematodes also enhanced the susceptibility of older plants to *V. albo-atrum*, the incidence of Verticillium-infected plants did not increase with time even though the number of galls per plant generally increased (compare Tables 2 and 3). Therefore, gall numbers per se probably were not responsible for the changes observed in susceptibility.

M. incognita acrita might enhance the susceptibility of plants to *V. albo-atrum* by providing infection courts for the fungus (3) and through its effect on cell walls (22) and on the physiology of the host (20, 23, 27). These possibilities have been considered in relation to the effect of *R. solani* on the susceptibility of cotton plants to *V. albo-atrum* (12). However, the influence of *M. incognita acrita* differed notably from that of *R. solani* in that plants treated with the largest concentrations of nematodes prematurely developed more severe symptoms of Verticillium wilt than did nontreated or Rhizoctonia-treated plants. Since this syndrome included early and severe defoliation, consideration should be given to the influence of the nematode on ethylene production and its role in this disease (6).

Field applications of the nematicide ethylene dibromide have not reduced the incidence of Verticillium wilt of cotton plants (14). However, recent field investigations involving chemical treatments of cotton plants indicate that a reduction in root-knot galling was associated with a reduction in the incidence of Verticillium wilt (16). Furthermore, preplant fumigations with the nematicide dibromoethane in the field delayed the incidence of Verticillium wilt development in the tomato cultivar 'Strano Special' (10). Our data, and those from the tomato studies (10, 21), also suggest that control of the root knot nematode could reduce the incidence of Verticillium-infected cotton plants.

Plant breeders should be aware of the possibility that a cultivar designated resistant to *V. albo-atrum*, when tested in soil free of *M. incognita acrita*, may prove to be susceptible under conditions of concomitant exposure to both the fungus and the nematode. Since large populations of this nematode may evoke more severe wilt symptoms than occur on plants infected only with *V. albo-atrum*, plants selected for resistance to *V. albo-atrum* in the presence of high root knot nematode populations might be particularly tolerant to this fungus in soils with low populations of the nematode.

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