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Competition Between *Tylenchorhynchus annulatus* and *Mesocriconema xenoplax* on Grain Sorghum as Influenced by *Macrophomina phaseolina*[1]

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Abstract: Greenhouse experiments were conducted to examine competition between *Tylenchorhynchus annulatus* and *Mesocriconema xenoplax* on grain sorghum roots that were colonized by the fungus *Macrophomina phaseolina* or free from fungus colonization. An incomplete factorial treatment design consisted of two levels of *M. phaseolina* (0 or 10 colony-forming units/g soil) and 12 *T. annulatus:M. xenoplax* ratios: 1,000:0; 750:0; 500:0; 250:0; 0:0; 0:250; 0:500; 0:750; 0:1,000; 750:250; 500:500; and 250:750. Plants were harvested after 105 days. Despite similar feeding habits, competition between these ectoparasitic nematode species was limited. *Tylenchorhynchus annulatus* was more susceptible to antagonism by *M. xenoplax* than the reverse, but susceptibility depended on initial inoculum ratio. Root colonization by *M. phaseolina* reduced competitive effects of *T. annulatus* on *M. xenoplax* but not the reverse. Both nematode species reduced shoot dry weight but only *T. annulatus* reduced root dry weight. Both plant weight parameters were reduced by *M. phaseolina.*

Key words: charcoal rot fungus, community ecology, competition, interaction, *Macrophomina phaseolina, Mesocriconema xenoplax,* nematode, ring nematode, *Sorghum bicolor,* stunt nematode, *Tylenchorhynchus anulatus.*

The stunt nematode, *Tylenchorhynchus annulatus* (Casidy) Golden, and the ring nematode, *Mesocriconema xenoplax* (Raski) Loof & de Grisse (= *Criconemella xenoplax* (Raski) Luc & Raski), are the most abundant nematode species on grain sorghum (*Sorghum bicolor* (L.) Moench.) hybrids in Louisiana (I. Wenefrida, unpubl. data). *Tylenchorhynchus annulatus* is distributed widely in tropical and subtropical areas of the world (Anderson and Potter, 1991). Lateral root feeding by this species results in root pruning, and heavy root-tip feeding causes severe stunting and necrosis. *Mesocriconema xenoplax* has a broad host range that includes grain sorghum (Westcott and Zehr, 1991; Zehr et al., 1986, 1990). This nematode species has been implicated as a component of peach tree short life syndrome (Nyczepir et al., 1983). Both nematodes are ectoparasites, which suggests that they may be in direct competition as they feed on grain sorghum roots.

Charcoal rot is caused by the fungus *Macrophomina phaseolina* (Tassi) Goid. and is a serious disease of grain sorghum throughout the world (Frederiksen, 1986; Mughogho and Pande, 1983). Lodging as plants approach maturity is the most diagnostic symptom of this disease (Hsi, 1956, 1961; Mihail, 1992), but other symptoms include decayed roots, premature stalk death, and poorly developed panicles with low-quality grain (Hsi, 1956; Mughogho and Pande, 1983). Diagnostic signs are small, black microsclerotia that are abundant in root and stem tissue of diseased plants. Disease severity is known to be directly related to plant stress, particularly high temperature and low soil moisture when they occur after flowering (Norton, 1958). Yield losses as great as 64% have been reported, although typical losses are lower (Frederiksen, 1986; Mughogho and Pande, 1983).

Competition between certain species in *Tylenchorhynchus* and *Mesocriconema* has been examined in greenhouse studies (Johnson, 1970). Competition between *T. martini* and *M. ornatum,* as measured by reduction in

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nematode numbers, was greater than that between *T. martini* and *Belonolaimus longicaudatus* or *M. ornatum* and *B. longicaudatus*. Results, however, depended on cultivar. Recently we described effects of *M. xenoplax, T. annulatus,* and *M. phaseolina* on grain sorghum growth and yield, as well as nematode reproduction (Wenefrida et al., 1997). Because our goal in that study was to evaluate combined effects of *M. xenoplax* and *T. annulatus,* these nematode species were not examined individually. Therefore, the objectives of the current study were to (i) determine the nature of competition between *M. xenoplax* and *T. annulatus,* (ii) examine effects of *M. phaseolina* on this competition, and (iii) evaluate individual and combined effects of these three pests on grain sorghum growth in greenhouse tests.

Materials and Methods

Fungus inoculum: Isolate Mp4 of *M. phaseolina* was collected in 1991 from the lower stem of a grain sorghum plant at Winnsboro, Louisiana, in a field that had been cropped continuously to grain sorghum for 12 years. The fungus was maintained at 4 °C as mycelia and microsclerotia on wood toothpicks (Mihail, 1992). To produce inoculum in quantity, 20 to 25 agar plugs (5-mm diam.) were transferred from 5- to 7-day-old cultures to glass trays containing 300 g corn cob grits that were ground to pass through a 250-µm-pore sieve (Bio-Serv, Frenchtown, NJ) and moistened with 1 liter potato dextrose broth (Difco, Detroit, MI). Moistened grits were autoclaved prior to introduction of *M. phaseolina.* This mixture of mycelia, microsclerotia, and grits was incubated at 30 °C for 60 days, dried in a forced-air oven at 30 to 35 °C for 3 days, and powdered with a mortar and pestle. Numbers of colony-forming units (cfu) per g dry inoculum were determined by dilution plating on potato dextrose agar (Difco, Detroit, MI) amended with rifampicin (100 mg dissolved in 1 ml dimethyl sulfoxide), metalaxyl (224 mg a.i. as Ridomil 2E-G), and Tergitol NP-10 (1 ml). Rifampicin, metalaxyl, and Tergitol were added after the medium was autoclaved and cooled to 55 °C (Cloud and Rupe, 1991).

Nematode inoculum: Both *T. annulatus* and *M. xenoplax* were separated by hand from mass extractions that contained small numbers of lesion and spiral nematodes. Monoxenic cultures of these two parthenogenetic nematode species were derived from single females, identified (Anderson and Potter, 1991; Raski and Golden, 1965), maintained in a greenhouse on grain sorghum hybrid Pioneer 8333, and used in all experiments.

Experimental design: Studies were conducted during 1995 in a greenhouse wherein temperatures ranged from 25 to 35 °C. Supplemental lighting from fluorescent and incandescent sources (ca. 260 $\mu E \cdot m^2 \cdot s$) provided a minimum of 16 hours of light daily. Soil in all tests was a Convent silt loam (coarse-silty, mixed, non-acid, thermic Aeric Fluvaquent; 80% sand, 6% silt, 14% clay) that was fumigated with methyl bromide (98% methyl bromide, 2% chloropicrin) at a rate of 1.6 g/kg soil prior to use. Clay pots were 15 cm in diam. and contained 1.5 kg soil. Seeds of grain sorghum hybrid Pioneer 8333 were germinated on moist filter paper in darkness at 30 °C and then sown in flats of fumigated soil in a greenhouse. Two weeks later, uniform seedlings were transplanted singly to pots. Soil was amended with 112.5 kg/ha each N (as ammonium nitrate) and K (as potassium chloride) according to soil test recommendations. Half of the fertilizer was added to soil at transplanting, and the remainder was added 7 days later.

Fungus and nematode treatments in a 2 × 12 incomplete factorial arrangement were examined in randomized complete blocks with four replications. Fungus treatments were soil that was not infested or infested with *M. phaseolina* at a rate of 10 cfu/g soil. This level was chosen based on the average infestation level for grain sorghum fields in Louisiana (J.S. Russin, unpubl. data). Powdered inoculum of *M. phaseolina* was thoroughly mixed with soil in a portable cement mixer to achieve uniform soil infestation at the appropriate level. Nematodes were introduced into pots at one of the following 12 *T. annulatus:M. xenoplax* ratios: 1,000:0, 750:

0; 500:0; 250:0; 0:0; 0:250; 0:500; 0:750; 0:1,000; 750:250; 500:500; and 250:750. The maximum nematode density introduced was 1,000 individuals/pot. This level was chosen based on average nematode populations in Louisiana grain sorghum field soils (I. Wenefrida, unpubl. data). Nematode inoculum was added 4 days after transplanting. Suspensions containing appropriate numbers of nematodes were pipetted into four depressions (1 cm in diam., 4 and 10 cm deep) surrounding the base of each seedling. Following infestation, depressions were filled with soil appropriate for the *M. phaseolina* treatment. This experiment was conducted twice.

Data collection and analysis: Plants were harvested 105 days after transplanting in both tests. Shoots were excised 2.5 cm above the soil line, and dry weights for roots and shoots were recorded after drying at 60 °C for 72 hours. Four soil cores (2.5 cm in diam. by 12.5 cm deep) were collected from each pot at harvest, and nematodes were extracted from 100-g subsamples with a centrifugal flotation technique (Jenkins, 1964). Adults and juveniles of each nematode species were counted, and population totals per pot as well as reproductive value (R, where R = Pf/Pi, Pf = final population density, and Pi = initial population density) were computed. Root systems were gently washed with water. Root colonization by *M. phaseolina* was determined according to published methods (Wenefrida et al., 1997). Treatment effects were determined with the General Linear Models procedure of SAS (SAS Institute, Cary, NC). When the number of treatment levels exceeded two, means were separated with the Tukey-Kramer test.

Results

Analyses showed no test by treatment interactions for any of the dependent variables measured in these studies. Therefore, results from duplicate tests were combined for final analysis. Root colonization by *M. phaseolina* averaged 70% to 75% in both tests and was not affected by either nematode species (data not presented). When *M. phaseolina* was absent, final population totals for *T. annulatus* without competition from *M. xenoplax* were similar at the three highest initial inoculum levels (1,000:0; 750:0; and 500:0) and reduced only at 250:0, the lowest inoculum level (Fig. 1A). Competition from *M. xenoplax* reduced *T. annulatus* final population totals when *T. annulatus:M. xenoplax* ratios were 750:250 and 500:500 but not at 250:750, the lowest ratio (Fig. 1A). Root colonization by *M. phaseolina* consistently reduced *T. annulatus* population totals, regardless of whether this nematode species was inoculated alone or with *M. xenoplax* (Fig. 1A). This reduction averaged 37% across all treatments.

Final population totals for *M. xenoplax* generally were lower than those for *T. annulatus* (Figs. 1A,B). When *M. phaseolina* was absent, final population totals for *M. xenoplax* without *T. annulatus* were similar at the three highest initial inoculum levels (0:1,000; 0:750; and 0:500) and were reduced only at 0:250, the lowest inoculum level (Fig. 1B). Final population totals for *M. xenoplax* were reduced by *T. annulatus* only at 250:750, the highest *T. annulatus:M. xenoplax* inoculum ratio (Fig. 1B). Other inoculum ratios that combined lower *M. xenoplax* levels with higher *T. annulatus* levels (i.e., 500:500 and 250:750) resulted in final population totals for *M. xenoplax* that did not differ from those obtained in the absence of *T. annulatus* (Fig. 1B).

Effects of *M. phaseolina* on *M. xenoplax* were more variable than those on *T. annulatus*. Root colonization by *M. phaseolina* consistently reduced *M. xenoplax* population totals at all inoculum levels as well as all *T. annulatus:M. xenoplax* inoculum ratios (Fig. 1A). This reduction averaged 36% across all treatments. However, significant interactions were detected between *M. phaseolina* and *M. xenoplax* that were dependent on nematode inoculum ratio. The competitive effect of *T. annulatus* to reduce *M. xenoplax* numbers at the 250:750 inoculum ratio was eliminated in roots colonized by *M. phaseolina* (Fig. 1B). An additional interaction was detected at the *T. annulatus:M. xenoplax* ratio of 750:250. The antagonistic effect of *M.*

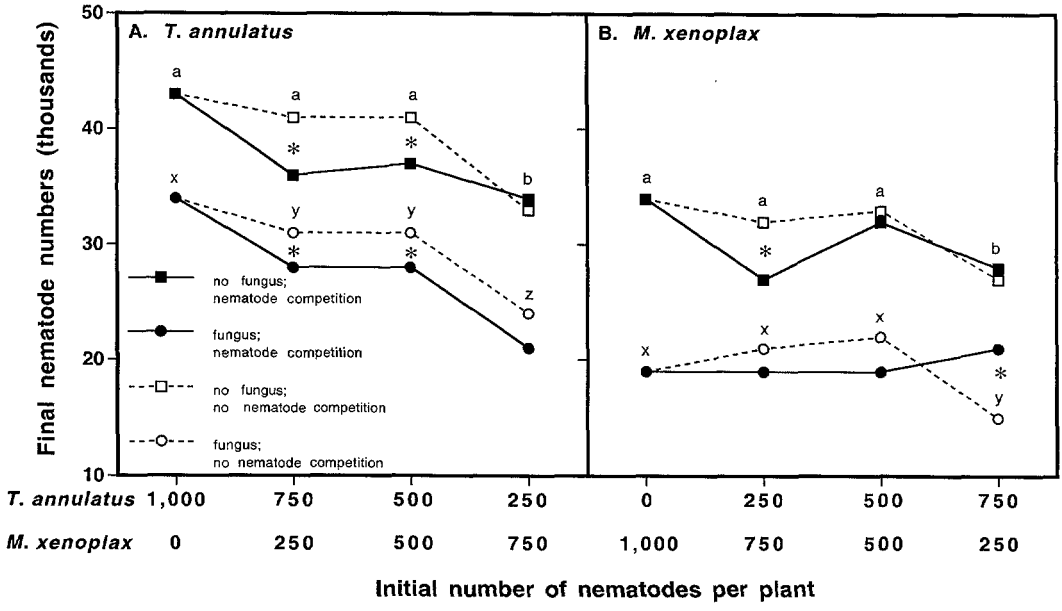

FIG. 1. Final numbers of *Tylenchorhynchus annulatus* and *Mesocriconema xenoplax* on grain sorghum roots colonized by the fungus *Macrophomina phaseolina* or free of fungus colonization. Nematode species were introduced individually (hollow symbols) at different inoculum levels or together (solid symbols) at different inoculum ratios. For lines described by hollow symbols, letters above symbols indicate means that differed significantly ($P \leq 0.05$) in response to inoculum level. For lines described by solid symbols, asterisks indicate inoculum ratios at which means for a nematode species without competition differed significantly ($P \leq 0.05$) from those with competition from another nematode species.

phaseolina on *M. xenoplax* populations at 0: 250 was significantly lessened when this nematode species competed with *T. annulatus* (Fig. 1B).

Reproductive (R) values for both *T. annulatus* and *M. xenoplax* increased consistently as levels of initial inoculum for both species decreased (Figs. 2A,B). This was true for inoculations involving either one or both nematode species. Competition had no effect on R value for either *T. annulatus* or *M. xenoplax* (Figs. 2A,B). Root colonization by *M. phaseolina* consistently reduced R values for both nematode species at all inoculum levels as well as all *T. annulatus:M. xenoplax* inoculum ratios (Figs. 2A,B). No interactions for R value were detected between *M. phaseolina* and either nematode species.

Tylenchorhynchus annulatus and *M. xenoplax* had similar effects on grain sorghum shoot dry weight. When *M. phaseolina* was absent, both nematode species reduced shoot dry weight relative to that for control plants without nematodes (Table 1). The magnitude of this reduction (about 40%) was similar regardless of initial nematode inoculum level or *T. annulatus:M. xenoplax* inoculum ratio. Results differed in soil infested with *M. phaseolina*. When nematodes were absent, *M. phaseolina* alone reduced shoot dry weight 45% (Table 1). There was no further decrease in shoot dry weight when *T. annulatus, M. xenoplax,* or both were combined with *M. phaseolina.*

Effects of *T. annulatus* on root dry weight varied with initial inoculum level. Weights were reduced following inoculation with *T. annulatus* at higher levels (1,000:0 and 750: 0) but did not differ from controls at lower levels (500:0 and 250:0) (Table 2). However, competition with *M. xenoplax* eliminated this effect. Root dry weights at all *T. annulatus:M. xenoplax* inoculum ratios did not differ from those of control plants without nematodes (Table 2). When nematodes were absent, *M. phaseolina* reduced root dry weight 35% (Table 2). No further decrease in root dry weight was detected when *T. an-*

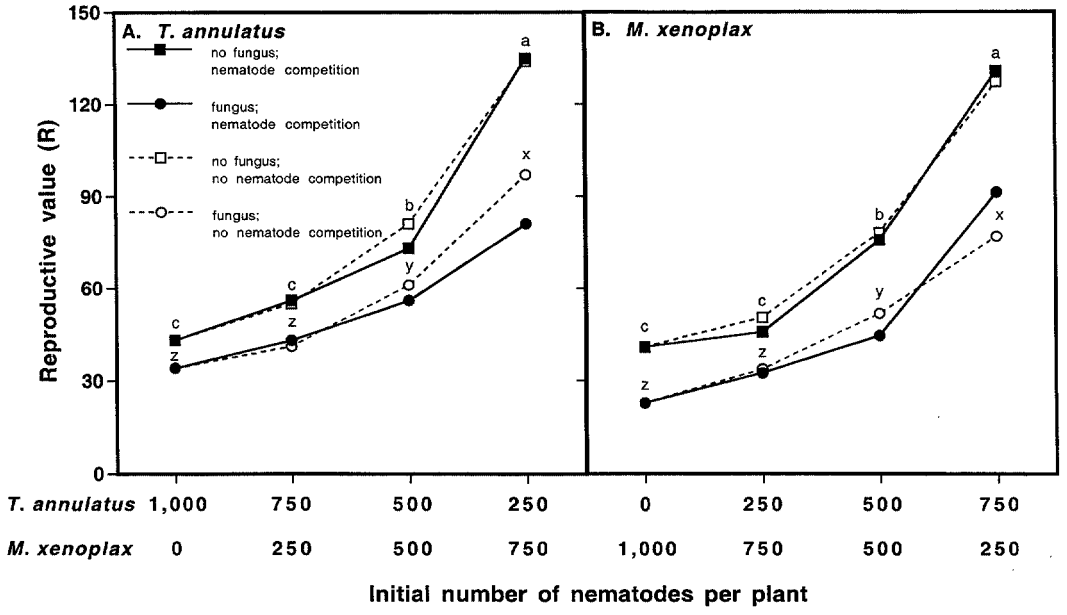

FIG. 2. Reproductive (R) values for the nematodes *Tylenchorhynchus annulatus* and *Mesocriconema xenoplax* on grain sorghum roots that were colonized by the fungus *Macrophomina phaseolina* or free of fungus colonization. Nematode species were introduced individually (hollow symbols) at different inoculum levels or in competition together (solid symbols) at different inoculum ratios. For lines described by hollow symbols, letters above symbols indicate means that differed significantly ($P \leq 0.05$) in response to inoculum level. For lines described by solid symbols, there was no effect ($P > 0.05$) on R value caused by competition between nematode species.

nulatus alone or with *M. xenoplax* was combined with *M. phaseolina.*

Root dry weight was not affected by *M. xenoplax* (Table 2). Weights of inoculated plants did not differ from those of control plants without *M. xenoplax,* regardless of initial inoculum level, *T. annulatus:M. xenoplax* inoculum ratio, or *M. phaseolina* infestation.

TABLE 1. Grain sorghum shoot dry weight as influenced by the nematodes *Tylenchorhynchus annulatus* and *Mesocriconema xenoplax* and the fungus *Macrophomina phaseolina.*

T. annulatus:M. xenoplax inoculum ratio	Shoot dry weight (g)			
	T. annulatus		*M. xenoplax*	
	Fungus absent	Fungus present	Fungus absent	Fungus present
1,000:0	21.2 bA	21.0 aA	—[x]	—
750:0	19.2 bA	17.2 aA	—	—
500:0	21.4 bA	22.3 aA	—	—
250:0	23.8 bA	23.8 aA	—	—
0:0	35.4 aA	19.6 aB	35.4 aA	19.6 aB
0:250	—	—	23.5 bA	23.5 aA
0:500	—	—	21.0 bA	22.0 aA
0:750	—	—	19.0 bA	17.2 aA
0:1,000	—	—	21.0 bA	21.8 aA
750:250	19.6 bA	16.4 aA	22.1 bA	19.6 aA
500:500	22.0 bA	19.6 aA	21.7 bA	19.2 aA
250:750	22.4 bA	19.7 aA	19.6 bA	16.0 aA

Data are combined means of four replicates in each of two tests. Within each column, values followed by the same lowercase letter indicate no difference ($P > 0.05$) in shoot dry weight caused by nematodes, according to the Tukey-Kramer test. Within each nematode inoculum ratio, values followed by the same uppercase letter indicate no difference ($P > 0.05$) in shoot dry weight caused by *M. phaseolina,* according to the *F*-test.

[x] Not measured.

TABLE 2. Grain sorghum root dry weight as influenced by the nematodes *Tylenchorhynchus annulatus* and *Mesocriconema xenoplax* and the fungus *Macrophomina phaseolina.*

T. annulatus:*M. xenoplax* inoculum ratio	Root dry weight (g)			
	T. annulatus		*M. xenoplax*	
	Fungus absent	Fungus present	Fungus absent	Fungus present
1,000:0	16.3 bA	14.8 aB	—[x]	—
750:0	13.9 bA	17.5 aA	—	—
500:0	21.5 aA	18.6 aA	—	—
250:0	22.5 aA	15.5 aB	—	—
0:0	25.9 aA	16.9 aB	25.9 aA	16.9 aB
0:250	—	—	22.2 aA	17.5 aA
0:500	—	—	23.1 aA	14.0 aB
0:750	—	—	19.2 aA	14.1 aA
0:1,000	—	—	20.8 aA	15.7 aA
750:250	20.0 aA	16.0 aA	23.5 aA	14.2 aB
500:500	23.8 aA	14.2 aA	23.8 aA	14.2 aB
250:750	23.5 aA	14.2 aA	20.0 aA	16.0 aA

Data are combined means of four replicates in each of two tests. Within each column, values followed by the same lowercase letter indicate no difference ($P > 0.05$) in root dry weight caused by nematodes, according to the Tukey-Kramer test. Within each nematode inoculum ratio, values followed by the same uppercase letter indicate no difference ($P > 0.05$) in root dry weight caused by *M. phaseolina,* according to the *F*-test.

[x] Not measured.

DISCUSSION

The effects of nematode species on each other generally are related to their nature of parasitism. *Tylenchorhynchus annulatus* usually feeds only on epidermal cells and root hairs (Wyss, 1981). *Mesocriconema xenoplax* has feeding habits similar to those of *T. annulatus,* and it tends to feed for prolonged periods on single root cortical cells without destroying these cells (Westcott and Hussey, 1992). Relatively few reports have addressed competition with these nematodes. Chapman (1959) found that reproduction in the related species *Tylenchorhynchus martini* was reduced severely (75% to 90%) when this nematode was placed in competition with *Pratylenchus penetrans* on red clover. Effects of *M. xenoplax* on other nematode species have been inconsistent. Santo and Bolander (1977) found that *M. xenoplax* suppressed reproduction by *Meloidogyne hapla,* but Nyczepir et al. (1983) reported no effect of *M. xenoplax* on reproduction by *M. incognita.* Johnson (1970) found that both *M. ornatum* and *T. martini* were very susceptible to competition by *Belonolaimus longicaudatus,* but that these results depended on host cultivar.

Although it is generally accepted that competition tends to be greater between species with similar feeding habits, our results suggest that competition between these two ectoparasitic nematode species on grain sorghum was limited. In our study, *T. annulatus* was more susceptible to antagonism by *M. xenoplax* than the reverse, but susceptibility depended on initial inoculum ratio. At higher *T. annulatus* levels (750:250, 500:500), competition by *M. xenoplax* effected slight ($\leq$ 12%) but consistent reductions in *T. annulatus* population totals. The absence of this effect at the lowest *T. annulatus* inoculum level (250:750) suggests that host resources were sufficient at that inoculum level to allow normal population development by *T. annulatus* despite competition by *M. xenoplax.* Susceptibility of *M. xenoplax* to competition by *T. annulatus* also was dependent upon initial inoculum level, but effects were limited. Competition by *T. annulatus* effected a similar (12%) reduction in *M. xenoplax* population totals, but only when the initial inoculum level for *M. xenoplax* was highest (250:750). These results suggest that *M. xenoplax* may utilize host resources more efficiently than does *T. annulatus.*

Although many studies have examined effects of fungi on phytoparasitic nematodes,

few have addressed effects of these fungi on competition between nematodes. Effects of *M. phaseolina* on competition between *T. annulatus* and *M. xenoplax* differed based on the nematode species being considered. Root colonization by *M. phaseolina* had little if any effect on *T. annulatus*. The response of this nematode species to competition by *M. xenoplax*, in terms of both final population totals and R values, was similar regardless of root colonization by *M. phaseolina*. However *M. phaseolina* had more consistent effects on *M. xenoplax*. Root colonization by the fungus tended to reduce the competitive effects of *T. annulatus* on *M. xenoplax*. This was observed at both high (250:750) and low (750:250) *T. annulatus:M. xenoplax* inoculum ratios. In a recent study, Stetina et al. (1997) reported that the relationship between *Meloidogyne incognita* and *Rotylenchulus reniformis* on soybean was independent of colonization by the stem canker fungus *Diaporthe phaseolorum* var. *caulivora*.

Wenefrida et al. (1997) showed reductions in grain sorghum growth and yield caused by a nematode community comprised of both *T. annulatus* and *M. xenoplax*. Results from the present study expand on these findings and show further that both *T. annulatus* and *M. xenoplax* alone were pathogenic to grain sorghum. Both nematode species caused similar, consistent reductions in shoot dry weight. Reductions in root dry weight, however, depended on nematode species as well as inoculum level. Only *T. annulatus* reduced root dry weight, but these reductions occurred only at the highest *T. annulatus* inoculum levels and in the absence of competition from *M. xenoplax*.

For both shoot and root dry weights, the combined effects of *M. phaseolina* with these nematode species were less than the sum of the effect of each pathogen alone. Such antagonistic interactions can be caused by a spatial occupation or physical alteration of feeding sites, or by a physical alteration of the host that decreases its suitability (Powell, 1971). *Macrophomina phaseolina* is a root-inhabiting fungus with little or no saprophytic growth in either soil or dead host cells (Collins et al., 1991; Mihail, 1992). *Tylenchorhynchus* spp. commonly feed on epidermal cells and root hairs (Claflin, 1983; Wyss, 1981), whereas *Mesocriconema* spp. prefer cortical cells farther back in the root and form modified cortical food cells (Westcott and Hussey, 1992). The similarity in modes of parasitism of these three pathogens likely affected the degree of competition between the species and consequently the antagonistic interaction detected in the present study.

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