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# Replacement Series: A Tool for Characterizing Competition between Phytoparasitic Nematodes[1]

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*Abstract:* The replacement series approach was used to detect and define competition between *Meloidogyne incognita* (Mi) and *Rotylenchulus reniformis* (Rr) on soybean. In three greenhouse tests, soybean cv. Davis seedlings were inoculated with 1,000 vermiform nematodes in the following Mi:Rr ratios: 0:0, 100:0, 75:25, 50:50, 25:75, and 0:100. After 86 days, relative nematode-yield values (number of each species in mixed culture divided by number in nonmixed culture) were calculated based on nematodes in soil per gram of dry root tissue. Calculated values were plotted and the resulting line compared with a reference line representing equal inter- and intraspecific competition predicted by the replacement series. Relative yields for Mi were higher than predicted at all ratios where Mi and Rr occurred together (lack-of-fit regression, $F = 5.9401$, $P = 0.0008$), indicating increased reproduction in the presence of Rr. Relative yields for Rr did not differ from predicted yields (lack-of-fit regression, $F = 0.7565$, $P = 0.5203$), indicating no effect of Mi on Rr. These relationships were not detected using analysis of variance. The relationship between Mi and Rr was independent of host colonization by *Diaporthe phaseolorum* var. *caulivora,* the stem canker fungus.

*Key words:* competition, *Diaporthe phaseolorum* var. *caulivora, Glycine max, Meloidogyne incognita,* nematode, reniform nematode, root-knot nematode, *Rotylenchulus reniformis,* soybean, stem canker.

Root-knot (*Meloidogyne incognita* (Kofoid & White) Chitwood) and reniform (*Rotylenchulus reniformis* Linford & Oliviera) nematodes are pathogenic to soybean (*Glycine max* (L.) Merrill) (Sinclair and Backman, 1989). In Louisiana, nematode damage suppressed soybean yields 4% to 8% annually during 1988–1993 (Sciumbato, 1993; Wrather and Sciumbato, 1995). Cotton (*Gossypium hirsutum* L.), another major crop susceptible to damage by these nematodes (Overstreet and McGawley, 1995, 1996), is grown in many of the same areas in Louisiana as soybean. Since the host range and geographic distribution of root-knot and reniform nematodes overlap, it is likely that the two species compete for host root tissue.

Competition between nematodes typically has been evaluated by comparing the number of individuals recovered from the soil using analysis of variance (ANOVA) and appropriate post-ANOVA means separation procedures (Chapman and Turner, 1975; Dickson and McSorley, 1990; Gay and Bird, 1973; Guy and Lewis, 1987; Herman et al., 1988; Ibrahim and Lewis, 1986; Niblack et al., 1986; Thomas and Clark, 1983a, 1983b). However, a means comparison test may not account for differences in the reproductive capabilities of individual species.

Recently, the replacement series approach developed by plant ecologists (De Wit, 1960; De Wit et al., 1966) has been employed to study relationships between phytopathogenic fungi (Adee et al., 1990; Zitko and Timmer, 1994), epiphytic ice-nucleating bacteria (Wilson and Lindow, 1994b), and bacteria existing in the bean phyllosphere (Wilson and Lindow, 1994a). Replacement series experiments are designed to quantitatively assess the relative impact of inter- and intraspecific competition between two species at a single community density. Target species are introduced alone or together in various ratios. At the end of the experiment, relative nematode yields (number of each species in mixed culture divided by number in nonmixed culture) are calculated for each species. Inhibition or stimulation of a species can be visualized by plotting the relative nematode yields against the input proportion of that species (Fig. 1). If inter- and intraspecific competition are equal, final nematode population sizes for

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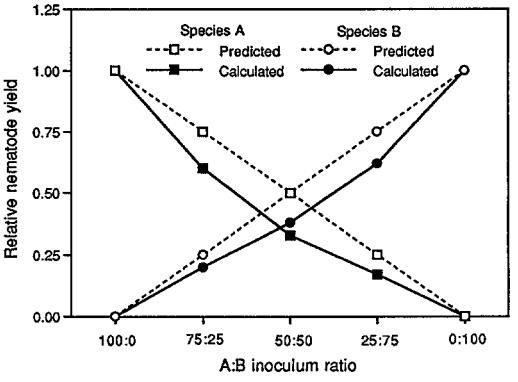


FIG. 1. Hypothetical replacement series between species A and B. Equivalence of inter- and intraspecific competition is indicated by dotted lines. Interspecific competition (inhibition) is illustrated by solid lines.

each species should be directly proportional to the percentage of that species initially introduced.

The primary objective of this research was to assess the usefulness of the replacement series approach in detecting and describing competitive relationships between root-knot and reniform nematodes. A secondary objective was to determine if the relationship between root-knot and reniform nematode differs on soybean colonized by the stem canker fungus, *Diaporthe phaseolorum* (Cke. & Ell.) Sacc. var. *caulivora* Athow & Caldwell (Dpc). A preliminary report has been published (Erwin et al., 1995).

## MATERIALS AND METHODS

*General procedures:* Experiments were conducted in a greenhouse, where temperatures ranged from 22 °C to 35 °C. Supplemental incandescent and fluorescent lighting (ca. 260 $\mu E \cdot m^{-2} \cdot sec^{-1}$) provided a minimum of 14 hours of light daily. In this experiment 15-cm-diam. clay pots were used that contained approximately 1.6 kg of a soil mixture composed of three parts fumigated (67% methyl bromide, 33% chloropicrin) Convent silt loam soil (Aeric Fluvaquent, coarse-silty, mixed, nonacid, thermic) and two parts autoclaved sand.

Soybean cv. Davis seeds were treated with a commercial preparation of *Bradyrhizobium japonicum* (Kirchner) Jordan (The Nitragin Co., Milwaukee, WI) and sown in flats. Seedlings of uniform size were selected when plants were at growth stage V1 (Fehr et al., 1971), and a single seedling was transplanted to each pot. Plants were fertilized every 14 to 21 days with 120 ml of a 23-19-17 N-P-K fertilizer solution (RapidGro; Chevron Chemical Co., San Ramon, CA), beginning at transplant. Plants received approximately 26 ppm N, 20 ppm P, and 33 ppm K at every fertilization.

Isolates of *M. incognita* race 2 and *R. reniformis* were derived from single egg masses and maintained on tomato (*Lycopersicon esculentum* L. 'Rutgers') in a greenhouse. Inoculum consisted of vermiform nematodes obtained from soil by hand-sieving and centrifugal flotation (Jenkins, 1964). Soil in each pot was inoculated with the required number of each species by pipetting nematodes suspended in tap water into two depressions made in the soil. Tap water was pipetted into depressions in control pots. Each depression was 1 cm in diameter, 4 cm deep, and 5 cm from the base of the stem on opposite sides of the plant. After inoculation, the depressions were filled with additional soil mix.

At the end of each experiment, five soil cores (2.5-cm-diam.) from the soil surface to the bottom of the pot were collected from each pot, mixed thoroughly, and subsampled (150 g) for nematode extraction. Nematodes were extracted by hand-sieving and centrifugal flotation. Numbers of juveniles, males, vermiform females, and swollen females collected on a 38-µm-pore sieve were recorded for each species.

Plant stems were cut at the soil surface, and the root-soil mass was removed from each pot. Root systems were freed from soil by gently washing in tap water. Galling severity was rated according to the following scale: 0 = no galls, 1 = galls less than 3 mm in diameter with no reduction in the number of feeder roots, 2 = galls 3 to 10 mm in diameter with no reduction in the number of feeder roots, 3 = galls 10 to 20 mm in diameter with no or slight reduction in the number of feeder roots, 4 = galls >20 mm in diameter with moderate reduction in the number of feeder roots, and 5 = galls >20

mm in diameter with major reduction in the number of feeder roots. Gall incidence was rated according to the following scale: 0 = no galls, 1 = galls confined to 25% or less of the root system, 2 = galls appearing over 26% to 50% of the root system, 3 = galls appearing over 51% to 75% of the root system, and 4 = galls appearing on 76% or more of the root system.

Nematode eggs were extracted from a subsample (2 g) removed at random from each root system following a procedure modified from Hussey and Barker (1973). Root tissue was stirred continuously for 10 minutes in 0.5% NaOCl and then poured onto nested 75- and 25-µm-pore sieves. Eggs collected on the 25-µm-pore sieve could not be identified to species, so egg counts were not included in population totals.

Cultures of Dpc were maintained on 2% water agar (WA) or potato dextrose agar (PDA) at room temperature (22–26 °C) in the laboratory. Fungus cultures were grown on PDA for 7 to 10 days before transferring to inoculum preparation plates. The toothpick inoculation procedure described by Russin et al. (1986) was employed. Inoculated plants received toothpick sections infested with Dpc (collected from soybean at the Burden Research Plantation, Baton Rouge, LA), whereas sterile toothpick sections were inserted into control plants.

Stem canker lesion length (mm) was recorded at 10-day intervals for 40 days, beginning 10 days after inoculation. Tissue sections collected from the margins of the lesion (symptomatic plants) or near the inoculation site (asymptomatic plants) were surface-disinfested by soaking for 5 minutes in a 0.5% NaOCl solution. Sections were rinsed in sterile distilled water, blotted on sterile paper towels, and plated on WA. Fungi growing from these sections were transferred to PDA and identified as Dpc based on colony morphology, development of pycnidia or perithecia, and morphology of conidia or ascospores.

*Replacement series experiments:* Nematode and fungus treatments in a factorial arrangement were examined using a randomized complete block design with five replications. Root-knot and reniform nematodes were introduced alone or in combination at an initial community density of 1,000 individuals per pot when plants reached growth stages V2 and V3. Inoculum was added at one of the following root-knot:reniform nematode ratios: 0:0, 100:0, 75:25, 50:50, 25:75, and 0:100. Forty-one days after inoculation with nematodes (growth stages R1 or R2 in tests 1 and 2), plants also were inoculated with Dpc. Experiments were terminated 84 to 86 days after nematode inoculation (growth stages R5 or R6 in tests 1 and 2, R2 in test 3). At harvest, plants were divided into root and shoot portions by cutting the stem at the soil line. Soybean root and shoot dry weights (after drying at 70 °C for 4 days) were recorded after galling assessment and collection of tissue samples for egg extraction and fungus reisolation. Soil samples were processed and nematodes counted. Relative nematode yield for each species at each inoculation density was calculated by dividing the number of nematodes of one species recovered from mixed culture by the number of nematodes of the same species recovered from nonmixed culture. This experiment was repeated (tests 1 and 2). After determining that the fungus did not affect the relationship between the nematodes, the experiment was conducted a third time with the Dpc treatment omitted (test 3). Ten replications were used in each experiment.

A preliminary experiment was conducted once to evaluate the accuracy of predicted relative nematode yields as dictated by the replacement series. The assumption was made in the replacement series that each species would yield in direct proportion to its initial inoculum level, so a stepwise, linear relationship in relative nematode yield is predicted. To document the reproductive capacity of each species, root-knot and reniform nematodes were grown in monospecific culture at inoculation densities of 1,000, 750, 500, and 250 per pot. Each treatment was replicated 10 times in a randomized complete block design. Relative nematode yield was calculated for each nematode species at each inoculation density by dividing the number of nematodes recovered in

low-density cultures by the number of nematodes recovered in the high-density culture.

*Data presentation and analyses:* To evaluate replacement series for assessing competition between root-knot and reniform nematodes, results obtained with this technique were compared with those from the traditional ANOVA. Analysis of variance and Tukey's HSD means separation procedures were performed on nematode numbers and relative nematode yields ("Fit Model" and "Fit Y by X" modules of SAS JMP, version 3.0) (SAS Institute, Cary, NC). Differences between the predicted relative yield lines defined by the replacement series and the relative nematode yield lines plotted using calculated relative nematode yield values were determined by lack-of-fit regression ("Fit Model" module of SAS JMP, version 3.0) (SAS Institute, Cary, NC). Paired *t*-tests ("Fit Y by X" module of SAS JMP, version 3.0) (SAS Institute, Cary, NC) were used to determine at which ratio(s) the predicted and calculated relative nematode yield values differed. Plant weights, galling indices, and stem canker lesion length data were subjected to analysis using ANOVA and Tukey's HSD means separation procedures so that values could be compared with those of the uninoculated control.

## Results

In monospecific culture, root-knot and reniform nematode relative yields were linear and proportional to initial inoculum levels. Lines based on calculated relative nematode yield values did not differ from those predicted by the replacement series for either root-knot or reniform nematode ($P \leq 0.05$). The relative nematode-yield lines predicted by the replacement series accurately represented the reproductive capability of the nematodes. Therefore, the predicted relative nematode yield values defined by the replacement series were used as the reference values in experiments involving combinations of these species.

In mixed species experiments, lack-of-fit regression indicated that the relative nematode yield line for root-knot nematode did not fit the reference line predicted by the replacement series ($F = 5.9401$, $P = 0.0008$) (Fig. 2). Paired *t*-tests established that the calculated relative nematode yields were higher than the predicted values at all ratios where root-knot and reniform nematode occurred together ($P \leq 0.05$). The apparent enhancement of root-knot nematode reproduction did not correspond to a decrease in the reniform nematode population; the calculated relative nematode yield line for this species did not differ from the reference line ($F = 0.7565$, $P = 0.5203$) (Fig. 2).

In tests 1 and 2, inoculation with Dpc resulted in measurable canker development 20, 30, and 40 days after inoculation. Canker lengths 40 days after inoculation, which represent the cumulative effect of the fungus, averaged 139.4 mm and were not influenced by infection of the host by either or both nematodes ($F = 1.3726$, $P = 0.2763$). Root, shoot, and total dry weights for plants inoculated with the fungus were 7.8, 3.8, and 11.6 g lower, respectively, than uninoculated controls (Table 1). Inoculation with Dpc limited galling severity and incidence (Table 1). An average of 500 fewer eggs were recovered per gram of root tissue from plants colonized by Dpc than from respective controls. In spite of stem canker symptom development and successful reisolation of the fungus from inoculated plants, Dpc did not

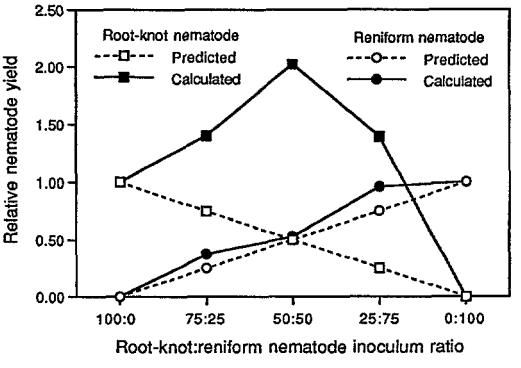


FIG. 2. Relative nematode yield of root-knot and reniform nematodes from soil 84 to 86 days after inoculation of 'Davis' soybean in greenhouse tests. Calculated data points are means of 30 replications in three tests. Predicted reference values indicate the expected response if inter- and intraspecific competition are equal.

TABLE 1. Influence of test, inoculation with *Diaporthe phaseolorum* var. *caulivora* (Dpc), root-knot:reniform nematode inoculum ratio, and their potential interactions on soybean cv. Davis weight, nematode soil population densities, relative yield values, and root galling induced by *Meloidogyne incognita* race 2 some 84 to 86 days after nematode inoculation in two greenhouse experiments.

| Treatment | Level | Dry weight (g) | | | Nematodes/g dry root | | Relative yield | | Root-gall rating | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Root | Shoot | Plant | Root-knot | Reniform | Root-knot | Reniform | Severity[a] | Incidence[b] |
| Test | 1 | 31.9 | 11.9 | 43.8 | 584 | 768 | 1.41 | 0.55 | 3.3 | 3.7 |
| | 2 | 17.8 | 21.5 | 39.3 | 2,109 | 4,461 | 1.57 | 0.88 | 2.7 | 3.2 |
| Dpc | Yes | 20.9 | 14.8 | 35.7 | 1,442 | 2,268 | 1.04 | 0.71 | 2.6 | 3.1 |
| | No | 28.7 | 18.6 | 47.3 | 1,252 | 2,961 | 1.94 | 0.72 | 3.3 | 3.8 |
| Mi:Rr | 0:0 | 23.4 | 24.8 a | 48.2 | — | — | — | — | — | — |
| ratio | 100:0 | 23.4 | 12.8 bc | 36.2 | 1,512 | — | 1.00 | — | 3.2 | 3.6 |
| | 75:25 | 21.7 | 11.7 c | 33.4 | 1,862 | 2,653 b | 1.74 | 0.37 b | 2.8 | 3.4 |
| | 50:50 | 34.9 | 15.9 bc | 50.8 | 979 | 2,078 ab | 2.05 | 0.48 a | 3.0 | 3.4 |
| | 25:75 | 23.4 | 15.3 bc | 38.7 | 1,034 | 2,653 ab | 1.18 | 1.00 a | 3.1 | 3.4 |
| | 0:100 | 22.3 | 19.6 ab | 41.9 | — | 4,619 a | — | 1.00 a | — | — |
| Source | | | | | | | | | | |
| Test | | *** | *** | NS | *** | *** | NS | NS | *** | * |
| Dpc | | ** | *** | *** | NS | NS | * | NS | *** | *** |
| Mi:Rr ratio | | NS | *** | * | NS | ** | NS | * | NS | NS |
| Test × Dpc | | NS | * | NS | NS | NS | NS | NS | ** | *** |
| Test × Mi:Rr ratio | | NS | NS | NS | NS | NS | NS | NS | ** | NS |
| Dpc × Mi:Rr ratio | | NS | NS | NS | NS | NS | NS | NS | NS | NS |

*, **, and *** indicate significant differences at $P \leq 0.05$, 0.01, and 0.001, respectively; NS indicates that means are not significantly different. For treatments with three or more levels, means followed by the same letter are not different (Tukey's HSD, $P \leq 0.05$).

[a] Severity is rated on a 0–5 scale where 0 = no galls and 5 = galls > 20 mm in diameter with major reduction in the number of feeder roots.

[b] Incidence is rated on a 0–4 scale where 0 = no galls and 4 = galls appearing on ≥76% of the root system.

affect root-knot or reniform nematode soil population densities, and no infestation ratio by fungus interactions were detected with regard to soil populations (Table 1). Relative nematode yields for Mi were lower for populations developing on plants with stem canker, but this effect was consistent across all nematode ratios (Table 1). Consequently, Dpc and related interaction terms were removed from the model and their associated variances pooled with that of the model error term. Data from tests 1 and 2 were pooled with data from test 3 for subsequent ANOVA and regression analyses.

Soybean root, shoot, and plant weights varied significantly among the three tests (Table 2). Nematode inoculum ratio did not impact root or plant weights but contributed to a significant test by ratio interaction with respect to shoot weight (Table 2). In two of the three tests, shoot weights were lower on plants inoculated with high levels (100:0, 75:25) of root-knot nematode ($P \leq 0.05$) (Fig. 3).

Nematode population densities and root-gall indices varied significantly between tests (Table 2). In general, reniform nematodes outnumbered root-knot nematodes in all mixed-species treatments. More reniform nematodes were extracted from pots inoculated only with this species than from pots containing mixtures of reniform and root-knot nematode (Table 2). The test by ratio interaction (Table 2, Fig. 3) indicated that severity of galling on plants colonized by both nematode species was generally equivalent to that seen on plants colonized only by root-knot nematode. The galling observed at the 25:75 ratio was lower than that seen at the 100:0 ratio in only one test ($P \leq 0.05$).

Relative yield values calculated for root-knot and reniform nematodes did not differ between tests (Table 2). Root-knot nematode relative yield values did not differ with respect to inoculum ratio (Table 2). However, reniform nematode relative yield values for the 75:25 ratio were lower than those for the 25:75 and 0:100 ratios (Table 2). No

TABLE 2. Influence of test, root-knot:reniform nematode inoculum ratio, and their interactions on soybean cv. Davis weight, nematode soil population densities, relative yield values, and root galling induced by *Meloidogyne incognita* race 2 some 84 to 86 days after nematode inoculation in three greenhouse experiments.

| | | Dry weight (g) | | | Nematodes/g dry root | | Relative yield | | Root-gall rating | |
|---|---|---|---|---|---|---|---|---|---|---|
| Treatment | Level | Root | Shoot | Plant | Root-knot | Reniform | Root-knot | Reniform | Severity[a] | Incidence[b] |
| Test | 1 | 31.9 a | 11.9 a | 43.8 a | 584 b | 768 b | 1.40 | 0.55 | 3.3 a | 3.7 a |
| | 2 | 17.8 b | 21.5 b | 39.3 a | 2,112 a | 4,474 a | 1.60 | 0.88 | 2.7 b | 3.2 ab |
| | 3 | 2.7 c | 5.6 c | 8.3 b | 137 b | 3,531 a | 1.37 | 0.72 | 1.5 c | 3.0 b |
| Mi:Rr ratio | 0:0 | 16.5 | 18.4 a | 34.9 | — | — | — | — | — | — |
| | 100:0 | 16.6 | 10.6 ab | 27.3 | 1,031 | — | 1.00 | — | 2.8 | 3.6 |
| | 75:25 | 15.7 | 9.6 b | 25.3 | 1,285 | 1,329 b | 1.40 | 0.37 b | 2.4 | 3.2 |
| | 50:50 | 24.1 | 12.4 b | 36.5 | 713 | 2,421 b | 2.02 | 0.53 ab | 2.4 | 3.2 |
| | 25:75 | 16.5 | 12.0 b | 28.5 | 750 | 2,886 b | 1.39 | 0.96 a | 2.4 | 3.1 |
| | 0:100 | 15.4 | 14.8 ab | 30.2 | — | 5,061 a | — | 1.00 a | — | — |
| Source | | | | | | | | | | |
| Test | | *** | *** | *** | *** | *** | NS | NS | *** | ** |
| Mi:Rr ratio | | NS | *** | NS | NS | *** | NS | ** | NS | NS |
| Test × Mi:Rr ratio | | NS | *** | NS | NS | NS | NS | NS | * | NS |

*, **, and *** indicate significant differences at $P \leq 0.05$, 0.01, and 0.001, respectively; NS indicates that means are not significantly different. Means followed by the same letter are not different (Tukey's HSD, $P \leq 0.05$).

[a] Severity is rated on a 0–5 scale where 0 = no galls and 5 = galls > 20 mm in diameter with major reduction in the number of feeder roots.

[b] Incidence is rated on a 0–4 scale where 0 = no galls and 4 = galls appearing on ≥76% of the root system.

test by ratio interactions were detected for relative yield of either species, which allowed pooling of data from all three tests for regression analyses.

## DISCUSSION

A relationship exists between root-knot nematode and reniform nematode on soybean cv. Davis, though the interpretation of the data depends largely on the analysis. Based on ANOVA, infection of host roots by root-knot nematodes suppressed reniform nematode populations, whereas root-knot nematode populations remained unaffected. Thomas and Clark (1983a) also documented a similar relationship between *M. incognita* race 1 and *R. reniformis* on sweet potato cvs. Centennial and Porto Rico. However, our results are likely a combination of inoculum level effects and the biological relationship between the species. When the same data are analyzed using the replacement series approach, the effects of initial inoculum level are eliminated, and the focus shifts to the biological relationship between the species. In our experiments, reniform nematode yields were directly proportional to the input ratio, suggesting that

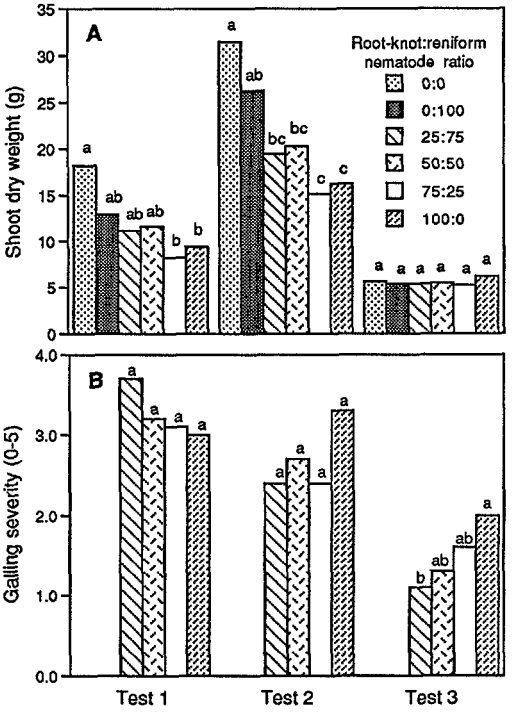


FIG. 3. Interaction between test and root-knot: reniform nematode inoculum ratio with regard to shoot dry weight (A) and severity of galling induced by *Meloidogyne incognita* race 2 (B) 84 to 86 days after nematode inoculation in three greenhouse tests; within each test, means with the same lowercase letter do not differ (Tukey's HSD, $P \leq 0.05$).

the apparent suppression of this species was really an artifact of inoculum level. Instead, we detected a significant increase in root-knot nematode relative yields whenever this species occurred in combination with reniform nematode. The mechanism for this increase, however, was not identified.

The replacement series approach goes a step beyond ANOVA in detecting and defining relationships between organisms. This method eliminates potential confusion associated with inoculum levels. Replacement series deal with proportions rather than actual numbers, are less sensitive to nematode population fluctuations between seasons and environments, and often allow data from several experiments to be combined, thus strengthening statistical tests. If the hypothesized reference lines are representative of the species employed in the study, as they were in this research, then any significant deviation from the reference lines will be related to a biological phenomenon rather than initial inoculum level. The reproductive capacities of the species under study should be compared with the hypothesized reference lines to be sure that these lines are appropriate. If the species in question do not conform to these lines, the replacement series approach may not be applicable.

Using a replacement series approach has several potential constraints. The results and their interpretation are density-dependent. Relationships detected at one initial community density may change dramatically if the density is altered. Care should be taken to choose one or more densities within the naturally occurring range for the species in question. For studies involving phytoparasitic nematodes, it is common to compare pathogen treatments with uninoculated controls to document the effects of the pathogen on parameters such as plant weight, yield, or symptom expression. Replacement series do not include such controls. Furthermore, it may not be possible to document the effects of a particular treatment on plant or symptom parameters without using ANOVA. In this research, the negative impact of Dpc on root-knot nematode relative yields and galling was not evident from the replacement series analysis. Finally, since relative yield values are ratios of final to initial levels of a pathogen or its propagules, they do not lend themselves to calculations involving plant or symptom data. We believe that employing a replacement series in addition to ANOVA will allow a more thorough examination of the biological system than either approach used alone.

Most significant interactions occur when pathogens infect the same region of the host (Powell, 1963, 1971). The fungus in this study colonizes the stem, a portion of the plant widely separated from the roots that harbor the nematode, so that any impact of the fungus on the nematodes or their relationship would have to be indirect. The lower relative nematode yields and suppressed galling on plants colonized by Dpc constitute the first report of this fungus inhibiting *M. incognita* race 2. A similar phenomenon was reported by Russin et al. (1989), who documented smaller *Heterodera glycines* Ichinohe population densities when nematodes developed on Dpc-colonized soybean cv. Bragg. We were not able to determine whether the inhibition of root-knot nematode resulted from fungal damage to host tissue, a change in host physiology induced by colonization with Dpc, induced resistance, or other unidentified factors. The relationship between root-knot and reniform nematode appears to be independent of host colonization by Dpc, since this fungus did not differentially alter either the population sizes or the relative yields of either nematode species.

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