Population Dynamics of Meloidogyne incognita and Rotylenchulus reniformis Alone and in Combination, and Their Effects on Sweet Potato[1]

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Abstract: Meloidogyne incognita (Mi) and *Rotylenchulus reniformis* (Rr) interactions on sweet potato were studied in naturally and artificially infested field plots for 3 years. In a naturally infested field, early season counts of Mi or Rr were positively correlated with later counts of the same nematode, but negative correlations were found between early Mi and subsequent Rr, and early Rr and subsequent Mi counts. In field plots fumigated with methyl bromide and then infested with low levels of Rr, Mi, and Rr + Mi, final population densities of Mi juveniles were reduced by Rr, but Rr was not affected by Mi. In field plots with a high natural population density of Rr, artificial infestation with high levels of Mi in both fumigated and nonfumigated treatments inhibited Rr, while the final Mi juvenile population density was not affected. Results indicate that a competitive interaction exists with each species capable of inhibiting the other and becoming the dominant population. The nematodes had no apparent effect on yield at the inoculum densities used, either alone or mixed. Both nematodes increased cracking of sweet potatoes, but mixed populations did not differ in incidence of cracking from either Rr or Mi alone. *Key words: Ipomoea batatas*, root-knot nematode, reniform nematode, interactions.

Journal of Nematology 15(2):204-211. 1983.

Meloidogyne incognita (Kofoid and White) Chitwood (Mi) and *Rotylenchulus reniformis* Linford and Oliveira (Rr), two of the dominant nematodes in tropical and subtropical areas worldwide, commonly occur together in the same field and on the same host (1,14,22,27). Little information is available, however, on their possible interactions on a particular host. If crop damage is to be predicted based on nematode population counts, an understanding of nematode behavior in polyspecific complexes is important.

Meloidogyne incognita, a serious pathogen of sweet potato (*Ipomoea batatas* Poir.), has been observed to reduce root yields (17) and has been associated with severe root cracking (20). Resistant cultivars have been developed (10,11,13). *Rotylenchulus reniformis* has also been associated with yield losses and poor quality of sweet potatoes (3). Recently, it was found that cracking of fleshy roots in the field and the greenhouse was associated with Rr and could be limited by soil fumigation (9,12). So far no resistant cultivars have been found. 'Goldrush' was reported to be a poor host for reproduction of Rr (19), but also is one of the most sensitive cultivars to damage by Rr (9).

Several workers have observed that Rr was the most abundant species in a field while *Meloidogyne spp.* stayed at low population densities (5,7). Soil sampling in a 10-year sweet potato rotation experiment (Martin and Birchfield, unpublished) in a field infested with both Rr and Mi suggested that Rr became the dominant species while Mi declined. Several greenhouse studies on possible interactions between Rr and *Meloidogyne spp.* gave contradictory results. Sometimes Rr was inhibited by Mi, while Mi was not affected by Rr (23). In other studies, Mi and *M. javanica* were inhibited and Rr was not affected (16,25). In a histopathological study on cowpea (24), root tissue reactions induced by Rr and *M. javanica* remained unique even when feeding in close proximity. The objective of this study was to determine if an interaction exists between Rr and Mi and, if so, its effects on yield and quality of sweet potatoes. Abstracts of this work have been published (28,29).

MATERIALS AND METHODS

Experiments were conducted on an Olivier silt loam (5% sand, 80% silt, and 15% clay) infested with Rr and Mi at Baton Rouge, Louisiana, in 1979, 1980, and

Received for publication 3 May 1982.

[1]Portion of Ph.D. dissertation by the senior author, Louisiana State University, Baton Rouge.

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We gratefully acknowledge the assistance of Dr. V. L. Wright, Department of Experimental Statistics, Louisiana State University, Baton Rouge, LA 70803.

1981. Sweet potatoes were grown on ridges 30 cm high and 61 cm wide with 122-cm row spacing. Plots were 3.7 m long, planted with 10 terminal vine cuttings 30 cm apart, and separated by 122 cm alleys.

Soil samples were taken approximately every 30 days using a 2-cm-d soil probe with five probes per plot to a depth of 15–20 cm. Samples were extracted for 4 min using a semiautomatic elutriator. Nematodes were passed through 425-μm sieves into a sample splitter, and 1/5 of the sample was collected on 38-μm sieves. The 38-μm sieve fraction was then processed using centrifugal flotation (sucrose sp. gr. 1.18) (15). Counts were made of Mi juveniles and Rr juveniles + young adults per 250 cm^3 soil. Root fragments collected on the 425-μm sieves were extracted in 0.525% sodium hypochlorite for 10 min for estimation of nematode egg populations (6,8). Eggs of the two species could not be distinguished in mixed population.

The 1979 field test was conducted in a field naturally infested with Rr and Mi. The experimental design was a complete randomized block with six replications and six cultivars (Porto Rico, Travis, Centennial, Goldrush, Jasper, and Jewel). Plots were planted on 18 May; soil was sampled 29 March, 18 May, 18 June, 17 July, and 17 August; and plots were harvested 17 September.

In 1980 and 1981, field plots were established by artificial infestation of plots after fumigation with 134 kg/ha Terr-O-Gas 67 (67% methyl bromide, 31.8% chloropicrin) injected 20 cm deep, using a single chisel. The beds were covered with 1.5-mil black polyethylene until 10 days prior to planting. Ethoprop (6EC) was sprinkled at the rate of 7.0 kg a.i./ha between the beds in 1980. Both tests were set up as completely randomized block designs with four replications in 1980 and six in 1981. Three cultivars—Porto Rico, Jasper, and Goldrush—were planted in 1980, and Porto Rico alone was planted in 1981. Treatments included inoculation with Mi alone, Rr alone, Rr + Mi, and noninoculated.

Inoculum of a Louisiana population of Mi (race 1) was increased by inoculating 23-day-old 'Rutgers' tomato seedlings with 10,000 eggs in 15-cm-d pots. After 43 days, soil in pots was combined, and infested roots were cut in small pieces and mixed with the soil. The egg and larval population density in the soil and roots was estimated, and uninfested tomato soil was used to dilute the inoculum. For the 1980 test, inoculum of a Louisiana population of Rr was increased by inoculating 'Centennial' sweet potato plants in 15-cm-d pots with Rr-infested soil from a greenhouse population 5–6 months prior to planting. For the 1981 test, flats of Rr-infested field soil were collected on 18 February, brought to the greenhouse, and planted with Porto Rico sweet potato cuttings for nematode increase. Prior to inoculation, infested soil from pots or flats was combined, and roots were cut up and mixed with the soil. Field plots were infested by distributing the Mi and/or Rr inoculum across wide furrows made in the beds. The beds were then reformed and planted. The inoculum level for both years was estimated as 100 Mi or Rr per 250 cm^3 soil in the upper 30 cm. Uninfested soil and tomato roots were added to all plots. In 1980, field plots were infested and planted 5 June, sampled for nematodes 27 June, 4 August, 29 August, and 6 October, and harvested 10 October. In 1981, plots were infested and planted 23 May, sampled for nematodes 16 June, 16 July, 14 August, and 14 September, and harvested 24 September.

In a second field test in 1981, a row was selected with a high natural population density of Rr (2,700/250 cm^3 on 8 April) but no detectable Mi. The experimental design was a complete randomized block with four replications. Half of the plots were fumigated with 1,3-dichloropropene (Telone II) at the rate of 46.7 l/ha with a hand held fumigation gun. *Meloidogyne incognita*-infested soil and roots were added to give a level of 4,000/250 cm^3 soil. Treatments included fumigation, nonfumigation, fumigation + Mi, and nonfumigation + Mi. Planting, soil sampling, and harvest dates were the same as for the first 1981 test. Vine growth was rated visually on 8 July on a relative scale (from 0 = no growth to 4 = greatest growth) when vine growth reached the middle of the rows.

In both 1981 tests, samples of small cull fleshy roots (2.5 cm d) were pureed in a

Waring blender, and nematodes and eggs were screened through 425-μm sieves onto 38-μm sieves, processed by sucrose centrifugal flotation, and stained with acid-fuschin-lactophenol. Also, larger marketable size fleshy roots were sliced in 0.5–1.0 cm sections and the number of mature Mi females was counted. Samples from the first test consisted of 100-g random samples of small fleshy roots and five US No. 1 fleshy roots from each plot. In the second test, samples consisted of one hand-dug plant from each plot from which all small fleshy roots were extracted and all marketable fleshy roots were sliced.

The 1980 and first 1981 tests were analyzed as factorial experiments with two levels of Mi (presence or absence), two levels of Rr (presence or absence), and three cultivars (1980 only). Nematode population data was also analyzed as a split plot over time with two levels of Mi and Rr, three cultivars (1980 only), and four sampling dates. The second 1981 test was analyzed as a factorial with two levels of fumigation (fum. and nonfum.) and two levels of Mi (presence or absence). Differences were significant at $P = 0.05$ unless otherwise stated.

RESULTS

1979 field test: There were no differences among cultivars for Rr population density. Travis had higher Mi juvenile counts in August (630/250 cm^3 soil) than any other cultivar except Porto Rico (293/250 cm^3). Nematode distribution was not uniform, and significant differences in population density were found between replications. On 18 May, Mi juveniles were detected in 5 of 36 plots and 2 of 6 replications while Rr was found in all plots. On 17 August, Mi juveniles were detected in 22 of 36 plots and all 6 replications. Early season counts of Mi or Rr were positively correlated with later counts of the same nematode, but negative correlations were found between early Mi and subsequent Rr and between early reniform and subsequent Mi counts (Table 1).

No differences for average total yield were found among cultivars. Porto Rico had a higher percentage of fleshy roots with cracks (23%) than the other cultivars which ranged from 2 to 8%.

1980 field test: Nematode population counts were not different among cultivars, therefore data for the three cultivars were pooled (Fig. 1A). *Meloidogyne incognita* juvenile population densities appeared to peak by 29 August and decline by 6 October, whether alone or mixed with Rr, but Mi was lower in combination with Rr for both sampling dates. *Rotylenchulus reniformis* with Mi was more numerous on 29 August than Rr alone, but by 6 October differences were not significant. When data for each cultivar were considered separately, however, the apparent stimulation of reniform by Mi on 29 August was not significant. Control plots averaged 300 Rr and 7 Mi per 250 cm^3 soil on the final sampling date. The interaction Mi treatment × Rr treatment × month was significant for both Rr ($P < .01$) and root-knot ($P < .03$) counts in soil. No differences were found between nematode-inoculated treatments for egg counts, but nematode treatments had more eggs than control plots on 29 August.

There were no differences in yield among treatments (Table 2). Treatments inoculated with Mi tended to have lower yields than treatments without Mi. There were differences in yield among cultivars, with Jasper the highest followed by Porto Rico and Goldrush. Root cracking associated with Rr, Mi, and combined treatments was greater than that of controls (Table 2).

1981 field test 1: Rotylenchulus reniformis in the mixed population was lower than Rr alone on 16 June and 14 August (Fig. 1B) but not different on 14 September. *Meloidogyne incognita* juvenile counts in mixed population were lower than Mi counts alone on the final sampling date. Egg counts for nematode treatments were not different from each other but were higher than controls on 16 July and 14 August.

Yield differences (Table 3) were not different between treatments and cracking was negligible. Nematode eggs and juveniles extracted from cull fleshy roots were higher in Mi and Rr + Mi treatments than in control or Rr treatments. Staining made genus identification difficult, but the majority of juveniles in the Mi treatments apparently were Mi. Few mature Mi fe-

Table 1. Pearson product-moment correlations (*r*) between initial population levels of *Rotylenchulus reniformis* (Rr) and *Meloidogyne incognita* (Mi) in a naturally infested sweet potato field and subsequent population levels (1979 field test).

Initial nematode parameter	Later nematode parameter	Correlation coefficients		
		June	July	August
May Mi	Mi	.13	.58	.71**
	Rr	−.22	−.41**	−.18
May Rr	Mi	−.13	−.32	−.46**
	Rr	.68**	.36*	−.15

*Significant at $P = 0.05$.
**Significant at $P = 0.01$.

males were found in fleshy root slices from marketable roots, and no differences were found.

1981 Field test 2: Fumigated plots averaged fewer Rr (9/250 cm³ soil) then nonfumigated plots (293/250 cm³ soil) on 16 June. In the nonfumigated treatment (Fig. 1C), Rr increased rapidly in July, dropped slightly in August, and rose again in September. *Rotylenchulus reniformis* followed a similar pattern in the nonfumigated + Mi treatment but was lower on 14 August and 14 September than the nonfumigated without Mi. *Rotylenchulus reniformis* density in the fumigated plots increased in a linear fashion until, by the end of the

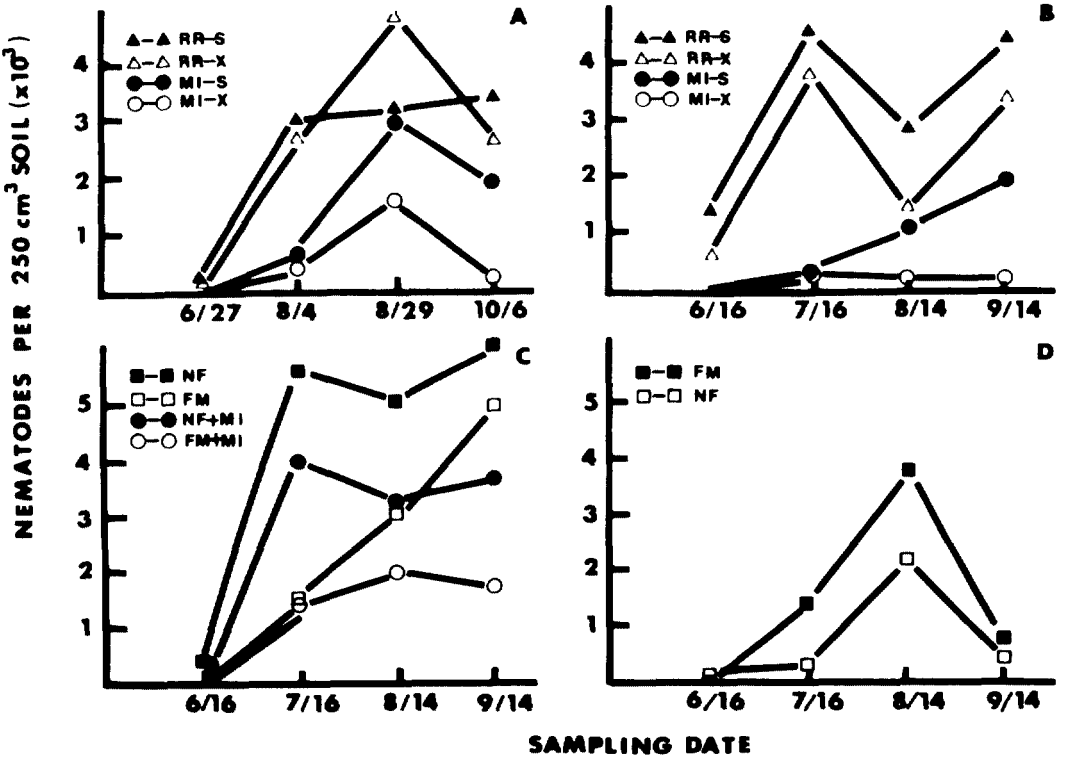

Fig. 1. Concomitant population dynamics of *Rotylenchulus reniformis* (RR) and *Meloidogyne incognita* (MI) on sweet potato. A) 1980 test and B) 1981 test fumigated with methyl bromide and artificially infested with low levels (100/250 cm³) of RR and/or MI. C) *R. reniformis* and D) *M. incognita* populations in second 1981 test in plots naturally infested with high levels of RR, fumigated with 1,3-dichloropropene, and artificially infested with high levels of MI (4000/250 cm³). S = single species, X = mixed infection. NF = nonfumigated, FM = fumigated.

Table 2. Effects of *Rotylenchulus reniformis* (Rr) and *Meloidogyne incognita* (Mi) on yield and fleshy root cracking of three sweet potato cultivars (1980 field test).

Treatment*	Cultivar	Avg. yield fleshy roots (kg/10 plants)	Percent cracking
Control	Porto Rico	7.3 bc†	13 de†
	Goldrush	4.3 ef	6 e
	Jasper	9.7 ab	18 cd
Rr	Porto Rico	7.3 bc	33 ab
	Goldrush	4.7 def	28 abc
	Jasper	10.7 a	21 cd
Mi	Porto Rico	6.9 cd	19 cd
	Goldrush	3.0 f	20 cd
	Jasper	7.7 bc	27 abc
Rr + Mi	Porto Rico	6.6 cde	23 bcd
	Goldrush	3.0 f	29 abc
	Jasper	8.4 abc	36 a

*Plots artificially infested with 100 Mi or Rr per 250 cm^3 in upper 30 cm. Treatment means are averages of four replicates.

†Column means followed by same letter not different ($P = 0.05$) according to Duncan's new multiple-range test.

season, counts were not different from counts in the nonfumigated plots. In the fumigated + Mi plots, Rr had similar counts the first two sampling dates, but by 14 September Rr was significantly lower than in the fumigated without Mi plots.

Counts of Mi juveniles in the nonfumigated plots were generally lower than Mi counts in the fumigated plots with a significant difference only on 16 July (Fig. 1D). Egg counts in the fumigated + Mi treatment for July and August averaged 2,024 and 4,732/250 cm^3 soil, respectively, compared to 1,065 and 2,042 for the nonfumigated + Mi treatment, but differences were not significant. Eggs and juveniles from cull fleshy root samples and mature Mi females in fleshy root slices were higher in the fumigated + Mi treatment than in the nonfumigated + Mi treatment (Table 4).

No differences were found for yields of fleshy roots (Table 4). The fumigated treatments had the higher yields and the nonfumigated + Mi treatment the lowest. The nonfumigated + Mi treatment had a lower vine growth rating on 8 July than any other treatment. Significant cracking was found

Table 3. Effect of *Rotylenchulus reniformis* (Rr) and *Meloidogyne incognita* (Mi) on yield, fleshy root cracking, and nematode counts in cull and marketable fleshy roots of Porto Rico sweet potato (1981 field test 1).

Treatment*	Avg. yield fleshy roots (kg/10 plants)	Percent cracking	Avg. nematodes per 100 g cull fleshy roots†	Avg. Mi females per fleshy root
Control	12.2 a‡	0.2 a‡	34 b‡	0 a‡
Rr	10.8 a	0.3 a	111 b	0 a
Mi	10.9 a	0.5 a	1676 a	3 a
Rr + Mi	11.1 a	0.7 a	965 a	2 a

*Plots artificially infested with 100 Mi and/or Rr per 250 cm^3 in upper 30 cm. Treatment means are averages of six replicates.

‡Column means followed by same letter not different ($P = 0.05$) according to Duncan's new multiple-range test.

†Includes eggs, root-knot, reniform, and saprophytic species.

Table 4. Effects of fumigation and artificial *Meloidogyne incognita* (Mi) infestation on yield, fleshy root cracking, and nematode counts in cull and marketable fleshy roots of Porto Rico sweet potato in field plots naturally infested with *Rotylenchulus reniformis* (1981 field test 2).

Treatment*	Avg. yield fleshy roots (kg/10 plants)	Percent Cracking	Avg. nematodes per 100 g cull fleshy roots†	Avg. Mi females per fleshy root
Fum.	10.2 a	3 b	258 b	0 b‡
Nonfum.	8.3 a	6 b	358 b	0 b
Fum. + Mi	9.4 a	22 a	3968 a	9 a
Nonfum. + Mi	7.5 a	25 a	956 b	3 b

Plots fumigated with 1,3-dichloropropene (46.7 liters/ha) and infested with 4000 Mi per 250 cm^3 in upper 30 cm. Treatment means are averages of four replicates.

†Includes eggs, Mi, Rr, and saprophytic species.

‡Column means followed by same letter not different ($P = 0.05$) according to Duncan's new multiple-range test.

only in plots infested with root-knot nematodes, whether plots were fumigated or not.

DISCUSSION

Negative correlations between early counts of one species and later counts of the other species in the study of Rr and Mi population dynamics in a naturally infested field suggested that a competitive interaction was occurring. *Rotylenchulus reniformis* appeared to be the dominant species, with Mi mainly detected late in the season in relatively low numbers. In some plots, however, where Mi was detected early in the season, Mi counts were highest and Rr counts were lowest at the end of the season.

Rotylenchulus reniformis apparently was inhibited very little when artificial infestation with relatively low levels of both species was used in controlled experiments in 1980 and 1981. In the final sampling for both years, there was no difference between Rr counts alone or in the presence of Mi. *Meloidogyne incognita* juvenile counts were suppressed by Rr at the end of the season. Egg counts from root fragments in soil samples were too variable to be of use in these tests, and eggs could not be distinguished by genus. Soil counts for Rr include larval stages, young females, and males, while soil counts for Mi include only second-stage larvae. The proportion of time spent in the soil is also greater for Rr than for Mi. Thus, soil counts probably more accurately represent the Rr population density than the Mi population density. Nevertheless, counts of Mi juveniles especially late in the season bear some correlation with the endoparasitic Mi population, and the suppression of Mi juvenile counts in the presence of Rr suggests that Rr is having some effect on Mi.

The significant interactions found between the Rr and Mi treatments also suggest that Mi and Rr affected each other's soil population density in the 1980 test and that Mi soil counts were affected by Rr in 1981.

The effect of higher initial inoculum level is apparent in results of the second 1981 field test. In this test, Mi juvenile counts in fumigated and nonfumigated plots were not different the last two sampling dates, while Rr was repressed by Mi. The suppression of Mi females in the fleshy roots in this test and the lack of suppression in the first 1981 test probably reflects the relative difference in population densities in the midseason samples.

The lack of significant yield differences among treatments may be attributed in part to the low inoculum levels used in the 1980 and first 1981 tests and to failure of the soil fumigant used in the second 1981 test to sufficiently reduce the initial Rr population density. The production of sufficient Rr inoculum in the greenhouse was a limiting factor.

Significant impairment in sweet potato quality, in the form of fleshy root cracking, occurred in 1980. These results support recent observations (9,12) that Rr can increase cracking, as has been reported pre-

viously for Mi (20). Cracking was not significant in 1981 except in Mi-treated plots in test 2. Cracking is generally favored by dry soil conditions followed by relatively high soil moisture during the period of fleshy root enlargement (21). Soil moisture conditions in 1980 followed this pattern. In 1981, however, there were no prolonged dry periods. When soil moisture patterns are conducive to growth cracking, root-knot or reniform nematodes may greatly increase the amount of cracking obtained. When soil moisture conditions are not conducive, however, the presence of nematodes may not be sufficient in itself to cause cracking.

Of the cultivars used, all are considered susceptible to reniform, with Goldrush the least suitable for reproduction and the most sensitive to damage (9). Jasper and Jewel have moderate resistance to Mi (13) but still support Mi reproduction. When two species such as Mi and Rr, both highly damaging to sweet potato, are found in the same field, cultivars resistant to just one species probably will be of little value unless used with soil fumigation.

The predominance of either Mi or Rr in a field probably is directly related to aspects of their life cycles that allow one or the other to be more competitive at a specific time. It has been observed (4,9), for example, that Rr numbers in fallow soil may remain very high through the winter and early spring, while Mi juveniles commonly die out and may not be detected in early season soil samples (our observations). A low survival rate of Mi and a high survival rate of Rr would favor the predominance of Rr in the field. *Meloidogyne incognita* is capable of producing many more eggs per egg mass than Rr. Reports have ranged from 30 to 200 for Rr (2,18), while Mi can produce more than 1,000 (26). In areas where Mi survival overwinter was high and it became well established early, then its higher reproductive capacity would favor it to predominate over Rr. The silt loam soil type in our tests could be more favorable for Rr than for Mi; studies should be tried on sandy soils.

In conclusion, both Mi and Rr are capable of suppressing each other's population density in field soil samples, and we have demonstrated both cases. Initial inoculum level appears to play a major role in determining which species will predominate. Whether sweet potatoes will be damaged more by a mixed infection of these two species than by either species alone is not clear, but in our studies there has been no indication that damage was affected by mixed infection.

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