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Competition between *Pratylenchus coffeae* and *Meloidogyne incognita*

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ABSTRACT

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Pratylenchus coffeae and *Meloidogyne incognita* were mutually antagonistic on mung bean roots. The penetration of both *P. coffeae* and *M. incognita* was significantly reduced when they were inoculated simultaneously comparing to when they were inoculated alone. In the simultaneous inoculation the number of sausage-shaped *M. incognita* was significantly lower than when *M. incognita* was inoculated alone, however, the percentage of *M. incognita* second-stage juveniles developed into sausage shape was not significantly different from that of the single inoculation. Inoculation simultaneously with the ratio of *P. coffeae* and *M. incognita* 750 : 250 or 250 : 750, resulted in significant suppression of penetration of both nematodes comparing to when they were inoculated alone. Two and 4 days prior inoculation of *P. coffeae* did not influence the late coming *M. incognita*, but prior inoculation of *M. incognita* inhibited the penetration of *P. coffeae*. The substance secreted by *M. incognita* or produced by the host in response to infection might have been involved in the latter case. Elucidating the substance responsible for the inhibition of *P. coffeae* might lead to a novel way of controlling the nematodes.

Key words: antagonistic, competition, *Pratylenchus coffeae*, *Meloidogyne incognita*

INTRODUCTION

Competition between organisms exists widely in nature. It has been known to exist among plants [7, 23], insects [25], entomopathogenic nematodes [18], bacteria [3], and even between sperms [11]. Competition between plant-parasitic nematodes were also observed [1, 2, 4, 5, 8, 10, 12, 14, 15, 16, 17, 20, 22].

In a field situation, it is not unusual to have more then one species of plant-parasitic nematodes. When the nematodes have overlapping host ranges, competition for food can be expected if the host plant tissues are insufficient for the existing nematode populations. When there is sufficient host root resource, or nematodes have different spatial aggregation niches, different nematodes species may coexist in a field. Bell and Watson [2] reported that no competition between *Paratrichodorus minor* and *Paratylenchus nanus* populations was found in a grazed pasture in New Zealand. Additionally, Brinkman, *et al.* [4] found no competition between *Heterodera arenaria* and *Meloidogyne maritime* on the natural dune grass *Ammophila arenaria*. However, there were more reports on competition [1, 4, 12, 20, 24] than lack of competition between nematodes.

Gay and Bird [12] found that population of *M. incognita* was inhibited by the presence of *Pratylenchus brachyurus* on cotton. Acosta and Ayala [1] reported that reproduction

of *Scutellonema bradys* was greatly inhibited by *P. coffeae* on Guinea yam. O'Bannon, *et al.*[20] found that *Radopholus similis* and *P. coffeae* inhibited each other on citrus. In addition, Yang, *et al.*[24] discovered that *M. incognita* and *Hoplolaimus galeatus* were mutually antagonistic on cotton. Brinkman, *et al.*[4] reported that *P. penetrans* suppressed the abundance of *H. arenaria* on the natural dune grass.

The interaction of different species of nematodes may not be always antagonistic to each other. Gay and Bird[12] reported that *M. incognita* increased the population of *P. brachyurus* on cotton when inoculated simultaneously or when *M. incognita* was inoculated first. The effect of nematodes on the host plant may be altered when two species of nematodes attack the same plant simultaneously. Griffin[13] studied the interrelationship of *M. hapla* and *Ditylenchus dipsaci* on the resistant and susceptible alfalfa and found a synergistic weight depression on Ranger, a cultivar susceptible to both nematodes, with simultaneous inoculation of the two nematode species.

P. coffeae (Zimmermann) Filipjev & Schuurmans Stekhoven and the root-knot nematode *M. incognita* (Kofoid & White) Chitwood are both important plant-parasitic nematodes in Taiwan. Understanding how they interact with each other is important for a successful nematode management strategy. The purpose of this study was to investigate the effect of simultaneous and sequential inoculation of *P. coffeae* and *M. incognita* on host penetration and nematode development under controlled conditions.

MATERIALS AND METHODS

Preparation of Nematodes

The lesion nematode *P. coffeae* was originally collected from the experimental station of the National Taiwan University and cultured on excised tomato roots in Gamborg's B5 medium (GIBCOBRL) following surface sterilization with H_2O_2 (3%) for 2 min. The nematodes from one-month old culture were extracted with modified Baermann funnels, collected daily and kept at 15℃. They were used within three days.

A population of *M. incognita* was also collected from the experimental station of the National Taiwan University and cultured on mung bean (*Vigna radiata* (L.) Wikzek) seedlings grown in Seed-Pack Growth Pouch (Mega International of Minneapolis). Egg masses were dissected from roots and hatched in a hatching chamber[21]. Fresh second-stage juveniles were collected every day to keep at 15℃, and were used within three days.

Preparation of seedlings

Mung bean seeds were surface sterilized with 70% ethanol for 4 minutes, rinsed three times with tap water, and sown in Seed-Pack Growth Pouch (Mega International of Minneapolis). Another batch of mung bean seeds, after surface sterilization, was sown in sterile sands in plastic cups. All of the above were kept at 28℃ in a growth chamber with 16 h photoperiod. The seedlings were used five days after sowing.

Effect on penetration

Experiment 1- Inoculation with equal numbers of both nematode species (500 nematodes each)

For the simultaneous inoculation, *P. coffeae* and *M. incognita* in 2ml suspension each were inoculated to a mung bean seedling in the growth pouch or in the cup with sterile sand. Two ml suspension of each species plus 2 ml of distilled water were inoculated as the control (single inoculation). For sequential inoculation, *P. coffeae* was inoculated 2 and 4 days prior to the inoculation of *M. incognita* to the mung bean seedlings in the growth pouches, or *vice versa*. The controls (single inoculation) of the prior species were inoculated at the same time as the sequential inoculation. The controls (single inoculation) of the later species were inoculated to the seedlings of 2- and 4-days older than those for the sequential inoculation, so that the age of the seedlings was the same as for the sequential inoculation.

Experiment 2- Inoculation with unequal numbers of nematode species (*P. coffeae*: *M. incognita* = 750 : 250 or 250 : 750)

The two species were inoculated simultaneously, or singly as the control, to the mung bean seedlings in the growth pouches.

All of the seedlings in experiments 1 and 2 were kept in the 28℃ growth chamber for 3 days after inoculation, or 3 days after the final inoculation in the sequential

inoculation treatments, and then the roots were stained with acid-fuchsin [6]. The nematodes in each root system were counted under a dissecting microscope (Olympus SZ61). There were four replicates for each treatment. Both experiments were repeated twice.

Effect on development and reproduction

The inoculation was done the same way as in the above for the simultaneous inoculation with equal numbers of each species to seedlings in the growth pouches. The plants were kept in the growth chamber for 10 days for the development test and 30 days for reproduction. After 10 days, the roots of the seedlings were stained with acid-fuchsin. The numbers of vermiform juveniles and the sausage-shaped juveniles of *M. incognita* were counted separately. As the counting of different stages of *P. coffeae* in the roots was too strenuous, the number of eggs in the roots was counted along with total number of nematodes instead. After 30 days, the numbers of galls and egg masses were counted. The number of adult females per root system was counted after teasing the root tissue apart to expose the females in the galls. There were four replicates for each treatment. The experiment was repeated twice.

One-way analysis of variance was carried out with SAS 9.1 software (SAS Institute, Cary, NC, USA) and treatment means were compared with t-test at the 95% level of confidence. Arcsine square root transformation was performed for percentages before statistical analysis. In the repeated experiment, the data were similar, so data from two experiments were pooled in the results.

RESULTS

The two nematodes species inside the mung bean roots could be separated by the different shapes of their tails after staining with acid-fuchsin (Fig. 1). The tail of *M. incognita* tapered gradually into a very pointed end while *P. coffeae* had a blunter tail. Therefore, the number of nematodes of each species could be counted accurately inside the same root system in the experiments.

In experiment 1, the number of *P. coffeae* penetrated the roots was significantly reduced when *P. coffeae* and *M. incognita* were inoculated simultaneously comparing to when *P. coffeae* was inoculated alone (Table 1). The average of 175 *P. coffeae* penetrated the roots in the single inoculation compared to only 58.3 nematodes penetrated the roots in the concomitant inoculation with equal numbers of *M. incognita*. The number of *M. incognita* penetrated the roots was significantly reduced when *P. coffeae* and *M. incognita* were inoculated simultaneously comparing to when *M. incognita* was inoculated alone (Table 1). There was no significant difference in penetration by *P. coffeae* when *P. coffeae* was inoculated 2 days or 4 days prior to the inoculation of *M. incognita*. However, when *M. incognita* was inoculated 2 days or 4 days prior to the inoculation of *P. coffeae* the inhibition on penetration of *P. coffeae* was significant (Table 1). There was no significant difference in penetration of *M. incognita* when *M. incognita* was inoculated 2 days or 4 days prior to or after the inoculation of *P. coffeae*.

In experiment 2, inoculation with unequal numbers of the two species, 750 *P. coffeae* + 250 *M. incognita* or 250 *P. coffeae* + 750 *M. incognita*, simultaneously resulted in

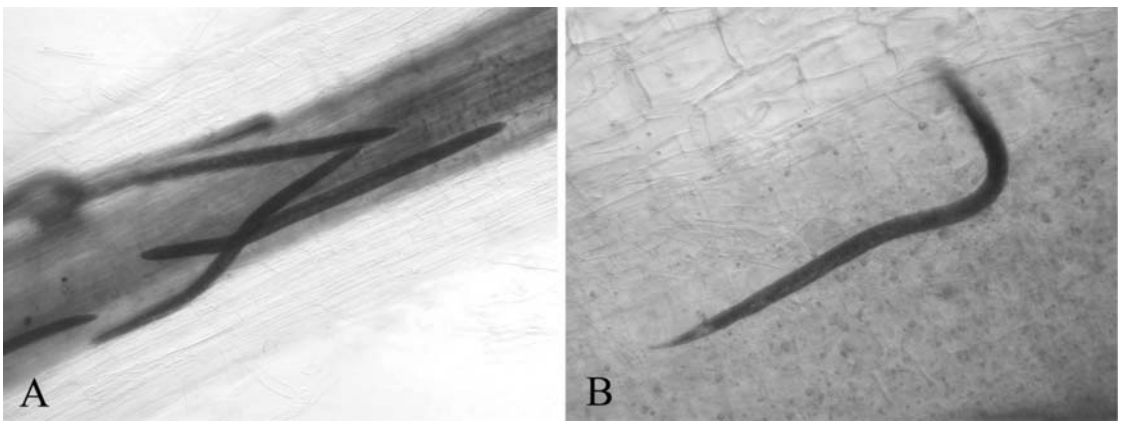

Fig. 1. The *Pratylenchus coffeae* had finger-like tail shape (A) and *Meloidogyne incognita* had tapering shape (B), nematodes were in mung bean roots after staining with acid- fuchsin.

Table 1. Effect of simultaneous and sequential inoculation with equal numbers of *Pratylenchus coffeae* (P) and *Meloidogyne incognita* (M) on penetration in mung bean roots

Treatment[1]	No. nematodes penetrated	
	M. incognita	*P. coffeae*
P+M	19	58.3
P		175
M	77.7	
t-test	*[2]	*
2dP+M	77	218
2dP		244.7
M	90	
t-test	ns[3]	ns
2dM+P	105	172
2dM	139.7	
P		249
t-test	ns	*
4dP+M	98	207
4dP		220
M	116	
t-test	ns	ns
4dM+P	105	159
4dM	121	
P		231
t-test	ns	*

[1] P+M: simultaneous inoculation; 2dP+M: *P. coffeae* inoculated 2 days prior to *M. incognita*; 2dM+P: *M. incognita* inoculated 2 days prior to *P. coffeae*; 4d P+M: *P. coffeae* inoculated 4 days prior to *M. incognita*; 4d M+P: *M. incognita* inoculated 4 days prior to *P. coffeae*.

[2] Two means within each pair are significantly different at 5% level according to t-test.

[3] Two means within each pair are not significantly different at 5% level according to t-test.

Table 2. Effect of simultaneous inoculation with unequal numbers of *Pratylenchus coffeae* (P) and *Meloidogyne incognita* (M) on penetration in mung bean roots

Treatment	No. nematodes penetrated	
	M. incognita	*P. coffeae*
750P+250M	9.6	143
750P		229
250M	45.5	
t-test	*[1]	*
250P+750M	38	23.3
250P		77.5
750M	141.2	
t-test	*	*

[1] Two means within each pair are significantly different at 5% level according to t-test.

significant suppression of penetration of both *P. coffeae* and *M. incognita* comparing to when they were inoculated alone (Table 2).

There were no significant difference between the penetration rates at inoculum levels of 250, 500, 750, and 1000 nematodes for either species of nematodes inoculated alone (data not shown).

The number of *M. incognita* developed into sausage shape in the simultaneous inoculation with *P. coffeae* was significantly lower than when *M. incognita* was inoculated alone (Table 3). However, because the penetration rate was lower in the simultaneous inoculation, the % development of *M. incognita* (No. sausage-shaped juveniles/Total no. nematodes penetrated) was not significantly different from that of the single inoculation.

The number of eggs of *P. coffeae* in the roots was significantly lower in the simultaneous inoculation with *M. incognita* then when *P. coffeae* was inoculated alone (Table 3). The total number of nematodes was also significantly lower in the simultaneous inoculation; there were 30.5 % and 24.3 % reduction for eggs and nematodes, respectively. The number of galls on the mung bean roots was significantly lower in the simultaneous inoculation than that in the single inoculation (Table 4), this was also true for the number of females and the number of egg masses.

The simultaneous inoculation in soil resulted in significant reduction of the number of nematodes penetrated the mung bean roots for both *P. coffea*e and *M. incognita* comparing to the respective single inoculation (Table 4).

DISCUSSION

P. coffeae and *M. incognita* were mutually antagonistic on mung bean roots. The penetration of both *P. coffeae* and *M. incognita* was significantly reduced when they were inoculated simultaneously comparing to when they were inoculated alone. Mutual antagonism between nematodes is one form of competition [(9)]. It has also been found between other nematodes. Estores and Chen [(10)] reported that *P. penetrans* and *M. incognita* depressed the population of each other in tomato. O'Bannon, *et al*, [(20)] found that mixed inoculation of *Radopholus similis* and *P. coffeae* on citrus resulted in lower populations of each species than in separate inoculation.

Although the use of growth pouches for the experiments saves labor and space, it is an artificial environment for the nematodes. To verify the results obtained in growth pouches, *P. coffeae* and *M. incognita* were inoculated to mung bean seedlings grown in sands simultaneously and alone. Significant mutual antagonism between the two species was found (Table 4). The results further confirmed the findings obtained in the growth pouches.

When there are enough penetration sites for all the nematodes encountering the roots simultaneously, mutual exclusion is not expected. Inoculation with 1000 *M. incognita* did not reduce the infection rate of *M. incognita* comparing to inoculation with 750, 500 or 250 nematodes (data not shown), and similar results were also observed on *P. coffeae*. These results indicated that there was no shortage of infection sites for the nematodes inoculated in the experiments. Therefore, the reduction of penetration of *P. coffeae* and *M. incognita* in the concomitant inoculation was the results of competition between the two species instead of lacking penetration sites. As to how *P. coffeae* and *M. incognita* interfered with each other when inoculated simultaneously remained an interesting question. It is not easy to investigate the nematode activities on the surface of the roots without proper equipment. It is common knowledge that animals fight for food. The fight exists even between small organisms like crickets. Nosil [19] reported that house crickets, *Acheta domesticus*, attacked each other for food by kicking, biting (mandible lunge), head charges, and wrestling. Whether microscopic animals like nematodes also attack each other physically on the surface of the roots is unknown. It would be an interesting case of animal behavior if it could be confirmed with proper equipment.

Competition of nematodes at penetration may not necessarily be linked to the subsequent development of nematodes. The data showed that the percentage of *M. incognita* second-stage juveniles developed into sausage shape was not significantly different between the simultaneous inoculatioin and the single inoculation experiment (Table 3). Similarly, Diez, *et al.* [8] found that the rate of development of *Rotylenchulus reniformis* was not affected by the presence of *M. incognita* on cotton although they were capable of inhibiting each other

Table 3. Effect of simultaneous inoculation[1] of *Meloidogyne incognita* (M) and *Pratylenchus coffeae* (P) on the development of *M. incognita*, egg production and total number of *P. coffeae* on mung bean roots

Treatment	*M. incognita*			*P. coffeae*			
	No. Sausage-shaped juveniles	% Penetration	% Development	No. eggs	Total no. nematodes	% Reduction of eggs	% Reduction of nematodes
M+P	24.2	6.3	76.6	299	162	30.5	24.3
M	85.1	21.0	81.1				
P				430	214		
t-test	*[2]	*	ns[3]	*	*		

[1] Each species had 500 nematodes.
[2] Two means are significantly different at 5% level according to t-test, arcsine square root transformation was performed for percentages before statistical analysis.
[3] Two means are not significantly different at 5% level according to t-test, after arcsine square root transformation.

Table 4. The effect of simultaneous inoculation[1] with *Pratylenchus coffeae* (P) on *Meloidogyne incognita* (M) galling and reproduction in mung bean roots and the penetration of both nematodes on mung bean roots in soil.

Treatment	In growth pouches			In soil	
	M. incognita			No. nematode penetrated	
	No. galls	No. females	No. egg masses	*P. coffeae*	*M. incognita*
M+P	23.2	17.7	14.5	67.0	24.5
M	47.8	43.1	38.8		89.9
P				162.1	
t-test	*[2]	*	*	*	*

[1] Each species had 500 nematodes.
[2] Two means within each pair are significantly different at 5% level according to t-test.

initially. Melakeberhan and Dey [16] also reported that competition between *H. glycines* and *M. incognita* had no effect on nematode development. In the present studies, there were eggs of *P. coffeae* in the roots at 10 days after the concomitant inoculation (Table 3), indicating that reproduction of *P. coffeae* occurred in the presence of *M. incognita*. The ratio of the total numbers of nematodes at 10 days after the concomitant inoculation to that in the single inoculation was higher than the ratio of those at 3 days after inoculation. This indicated that some eggs had developed into vermiform nematodes in the roots. Although development of *P. coffeae* were observed in the simultaneous inoculation, the percentage of development could not be calculated as for *M. incognita* (Table 3) because the initial inoculum was mixed developmental stages of *P. coffeae*.

It is conceivable that when one species outnumbers the other species it would be of advantage in the competition. The data showed that inoculation simultaneously with unequal numbers of the two species, 750: 250, resulted in significant suppression of penetration of the lesser species comparing to when they were inoculated alone (Table 2). The present findings are coincident with the report of Diez, *et al*. (8) where *Rotylenchulus reniformis* and *M. incognita* inoculated simultaneously on cotton inhibited each other when the amount of inoculum of one species was higher than the other.

Theoretically occupying the territory ahead of the other species should give advantage to the preinvading species, thus, timing was considered important to the outcome of competition between nematodes. Jatala and Jensen [14] reported that no significant population changes were observed for either *M. hapla* or *Heterodera schachtii* when they were inoculated simultaneously to sugar beets, but when *H. schachti* was inoculated 10 days earlier than *M. hapla*, the size of galls was significantly reduced. In addition, Gay and Bird [12] found that prior invasion by *M. incognita* suppressed *P. brachyurus* populations on tomato and that previous inoculation of *P. brachyurus* also inhibited root penetration by *M. incognita*. Umesh, *et al*. [22] reported that in experiments on competition between *P. neglectus* and *M. chitwoodi* in barley, the species that parasitized the roots first inhibited penetration of the latter species. The present findings showed that 2 and 4 days prior inoculation of *P. coffeae* did not influence the late coming *M. incognita*, but prior inoculation of *M. incognita* inhibited the penetration of *P. coffeae* (Table1). It appeared that the competition between the two nematodes occurred mainly on the surface of the roots, once one species has entered the roots, there was no longer interference on the root surface for the other species to utilize the infection sites. Similarly, Estores and Chen [10] reported that *P. penetrans* and *M. incognita* inhibited each other in tomato but there were no significant difference in the numbers of *P. penetrans* when they were inoculated 10 days prior to or after introduction of *M. incognita*. In the case where prior inoculation of *M. incognita* inhibited the penetration of *P. coffeae* in the present studies, other factors might have been involved. Estores and Chen [10] used split-root tomato plants to demonstrate that a transmissible substance, secreted by *M. incognita* or produced by the host in response to infection, was effective in reducing the penetration of *P. penetrans*. In the present study, the effect of the prior inoculation of *M. incognita* on *P. coffeae* penetration was effective in 5 days (2 days prior inoculation plus 3 days after inoculation of *P. coffeae*) which was faster than those reported by Estores and Chen [10] where it took 22 days (15 days prior inoculation plus 7 days after inoculation of *P. penetrans*). Elucidating the substance responsible for the inhibition of *P. coffeae* or *P. penetrans*, no matter it was secreted by *M. incognita* or produced by the host in reaction to infection, might lead to a novel way of controlling the nematodes.

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摘 要

蔡碧雲. 2008. *Pratylenchus coffeae* 與 *Meloidogyne incognita* 之間的競爭. 植病會刊 17 ：271-278.
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在綠豆根內 *P. coffeae* 與 *M. incognita* 之間存在著互相抑制的關係。同時接種兩種線蟲時 *P. coffeae* 及 *M. incognita* 之侵入率皆比單獨接種時爲低。同時接種兩種線蟲時發育成香腸狀之 *M. incognita* 三齡幼蟲數目比單獨接種時少，但幼蟲發育成香腸狀之比率與單獨接種時並無顯著差異。同時接種不相等數目的兩種線蟲，無論其佔有比率爲何其侵入率皆比單獨接種時爲低。先接種 *P. coffeae* 兩天或四天時，對 *M. incognita* 之侵入率無影響，但先接種 *M. incognita* 兩天或四天時，可降低 *P. coffeae* 之侵入率。此種影響可能牽涉到由 *M. incognita* 分泌而來或是由寄主對受感染所產生之反應而來之物質。深入探討此等可抑制 *P. coffeae* 侵入之物質，將可幫助新的線蟲防治方法之發展。

關鍵詞：競爭、抑制、*Pratylenchus coffeae*、*Meloidogyne incognita*