NEMATODES OF CASSAVA, MANIHOT ESCULENTA CRANTZ
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ABSTRACT

The plant-parasitic nematodes most frequently found associated with cassava, Manihot esculenta Crantz (syn. M. utiiimia Pohl.), throughout the world are: Pratylenchus brachyurus (Godfrey) Filipjev & Schuurmans Stekhoven, Rotylenchulus reniformis Linford & Oliveira, Helicotylenchus spp., Scutellonema spp., and Meloidogyne spp. Only P. brachyurus and Meloidogyne spp. are considered economically damaging to the crop, with root-knot nematodes the most widespread. Damage from Meloidogyne spp. usually depends on the population level, however the many differences in responses of various cassava cultivars to Meloidogyne species suggest that use of resistant or tolerant cultivars may be the most practical method for managing root-knot nematodes on this crop. Data are presented relating yield of the cassava cultivar ‘Senorita’ in southern Florida directly to weight of the seed piece and inversely to high populations of Meloidogyne incognita (Kofoid & White) Chitwood. Marketable yield of the cultivars ‘Senorita’ and ‘Mantiqueira’ were similar in plots having subthreshold levels of M. incognita, but ‘Senorita’ showed more galling than ‘Mantiqueira’, ‘HMC-2’, or ‘CMG-92’. The latter cultivar was poorly adapted to southern Florida conditions, and had the lowest yields of the cultivars tested.

Additional key words: Meloidogyne incognita, Rotylenchulus reniformis, Pratylenchus brachyurus, Helicotylenchus spp., Meloidogyne spp., tolerant cultivars, host-parasite relationships, root-knot nematodes, reniform nematode, lesion nematode.

RESUMEN

Se revisaron los nematodos parasiticos asociados con la yuca, Manihot esculenta Crantz (syn. M. utiiimia Pohl). Los nematodos exportados con mayor frecuencia a través del mundo en dicha cosecha son: Pratylenchus brachyurus (Godfrey) Filipjev & Schuurmans-Stekhoven, Rotylenchulus reniformis Linford & Oliveira, Helicotylenchus spp., Scutellonema spp., and Meloidogyne spp. Solo P. brachyurus y Meloidogyne spp. son considerados dañinos siendo el nematodo nodulador el más extendido. El daño del Meloidogyne spp. depende del nivel de la población y de la reacción de los cultivares de yuca a las especies del nematodo. Esto permite sugerir que el uso de
cultivares tolerantes o resistentes es el método más práctico para controlar el nematodo nodulador en esta cosecha. Se presenta la información sobre el cultivar comercial 'Señorita' del sur de la Florida que relaciona sus rendimientos directamente con el peso de la semilla o cangre, e inversamente con las poblaciones altas de Meloidogyne incognita (Kofoid & White) Chitwood. En otra prueba en el sur de la Florida los rendimientos de los cultivares 'Señorita' y 'Mantiqueira' fueron similares en parcelas con una población de M. incognita por debajo del nivel considerado peligroso pero 'Señorita' mostró de modo significativo (p = 0.05) más nódulos causados por M. incognita que 'Mantiqueira', 'HMC-2' o 'CMC-92'. Este último cultivar el más bajo rendimiento de todos los ensayados y parece pobremente adaptado a las condiciones del sur de la Florida.

Palabras claves adicionales: Meloidogyne incognita, Rotylenchulus reniformis, Pratylenchus brachyurus, Helicotylenchus spp., cultivares tolerantes, relaciones huésped-parásito, nematodo nodulador, nematodo reniforme, nematodo lesionador.

INTRODUCTION

Cassava, Manihot esculenta Crantz (syn. M. ultissima Pohl), is one of the more important starchy staples grown in the tropics (22). It is of particular value for its ability to produce a yield on nearly all soil types and to excel in production, compared to other crops, when grown on unused marginal soils. In addition to being an excellent source of low-cost carbohydrates, cassava has several other uses. Young leaves are very nutritious (51) and can be used as potherbs or as part of animal feed rations (9, 72), and the roots can be prepared in a similar manner as potato or can be converted to biofuels (79).

The plant-parasitic nematodes associated with cassava have been reviewed by Hogger (40), Dickson (30), and Roman (73). Hogger (40) presents a list of nematodes reported on the crop up to 1971. DeGuiran (28) has described the nematode fauna of Togo, giving particular emphasis to Pratylenchus brachyurus (Godfrey) Filipjev & Schuurmans Stekhoven. His information has been summarized by Merny (57) and by Niemann et al. (60). Caveness has worked extensively with nematodes on cassava in Nigeria and has recently summarized previous work with root-knot nematodes on the crop (17). In fact, a worldwide overview of cassava nematology would show a geographical bias toward western Africa because of the extensive efforts made in several countries of that region. Nematological work on cassava is presently increasing at a rapid pace throughout the world, and a number of controversial and conflicting findings have arisen. For these reasons, it is beneficial to bring together the previous information as well as to incorporate new research information into a unified summary of the nematode species associated with the crop.
Root-knot Nematodes (*Meloidogyne* spp.)

Root-knot nematodes were first observed on cassava by Neal in 1889 (39, 59) and are by far the most widely reported nematodes on the crop. *Meloidogyne arenaria* (Neal) Chitwood has been reported from Brazil (82), Fiji (44, 89), Nigeria (12, 13), and Philippines (26); *M. incognita* (Kofoid & White) Chitwood from Antigua (87), Brazil (10, 25, 82), Colombia (2), Fiji (44, 89), Florida (62), Honduras (69), Ivory Coast (31, 49, 65), Nigeria (4, 13, 15, 17, 65), Peru (83), Philippines (36, 37), Puerto Rico (73), Taiwan (83), and Tanzania (34); *M. incognita acrita* from Nigeria (13) and Malawi-Zambia-Zimbabwe (52, 53); *M. javanica* (Treub) Chitwood from Brazil (25, 82), Fiji (44, 89), Honduras (69), India (61), Ivory Coast (31), Malawi (74), Nigeria (4, 12, 13, 17), Philippines (36), and Togo (50). *Meloidogyne hapla* Chitwood has been mentioned in Brazil (82), and *Meloidogyne* spp. have been reported from Brazil (29, 86, 90), Dominican Republic (80), Fiji (5, 89), Florida (59), Ghana (32), Hawaii (66), Malaysia (71), Nigeria (13, 18, 45), Philippines (35, 84), Puerto Rico (7), Taiwan (42), and Trinidad (11).

Reports of the extent of damage to cassava by root-knot nematodes are often conflicting. Some sources (7, 71) do not consider them to be very damaging to the crop, and Roman (73) points out that cassava could be grown successfully in a sandy soil infested with *M. incognita* and other nematodes, while other crops could not. On the other hand, they are considered to be a serious problem in western Africa, particularly in Nigeria and Ivory Coast (65). Such conflicting opinions are probably due to the variable response of cassava to *Meloidogyne*, not only because of the different species and races of *Meloidogyne* that may be involved, but perhaps more importantly, because cassava cultivars may respond very differently to the same species, or to different population levels of root-knot nematodes. Nevertheless, the accumulated evidence suggests that *Meloidogyne* can cause serious problems to the crop and outlines conditions under which they can be damaging.

Root knot nematodes usually feed on the white feeder roots of cassava, producing galls of variable size containing 1-3 egg masses (71). In more severe infestations, smaller galls may coalesce to form elongated galls containing numerous egg masses. Yield of harvestable roots can be negligible in heavy infestations (65). Reduction in quality of marketable roots due to direct attack by root-knot nematodes is a point of concern (30), but the authors and others (4, 17) have not observed gall information on the enlarged storage roots. One of these observations was made on roots harvested 15½ months after planting in an inoculation test in which galling from *M. incognita* and *M. javanica* was evident elsewhere in the root systems (17), but not on the storage roots.
Much of the work done on the effects of root-knot nematodes on cassava has been carried out at the International Institute of Tropical Agriculture (IITA) in Ibadan, Nigeria, particularly by Caveness (15, 17, 18, 19). Early inoculation studies there revealed that cassava seedlings were highly susceptible to root-knot nematodes, and at the heaviest inoculum levels, the plants suffered reductions in height and storage root weight of 52% and 87%, respectively (3, 18). In another inoculation test, weight of storage roots was reduced by *M. javanica*, and also by *M. incognita* (race 2) either alone at a high inoculum level or in combination with *Pratylenchus sefaensis* Fortuner (4). More recently (17), a microplot experiment was carried out on two cultivars, ‘TMe 30572’ and ‘TMe 30572’ in which each were inoculated with 10,000 eggs of either *M. javanica* or *M. incognita* (race 2). Harvest of the plants after 15½ months revealed galling of the feeder roots of both cultivars, with slightly greater levels of galling from *M. incognita* than from *M. javanica*, an observation which has been made elsewhere (36). Nematodes reproduced well on both cultivars and *M. incognita* showed no differences in egg production by cultivar. *Meloidogyne javanica* produced more eggs on ‘TMe 30572’ than on ‘TMe 30555’, but even in the latter case, egg production averaged more than 100/g of root. Each species reduced stalk height, stalk weight, and weight of storage roots of each cultivar. Differences in stalk height and weight could be important in terms of producing quality planting pieces for the next season (19). The pooled data from this experiment suggested that the weights of the various plant parts varied with the number of *Meloidogyne* juveniles in the soil at harvest. No reduction in root weight was observed when populations were moderate (about 95 juveniles per 100cm² of soil). Very high populations (515/100cm²) reduced root weight to only 2% of that of uninoculated plants. Stimulation of plant growth by low nematode numbers has been suggested (17, 18). The effects of damage to cassava at higher *Meloidogyne* population levels have been corroborated by a test involving inoculation of ‘Golden Yellow’ cassava with various levels of *M. incognita* and *M. javanica* (36). After four months, inoculation levels of 10,000-20,000 *M. incognita* eggs/plant resulted in significant (P = 0.05) reductions in total root weight, weight of enlarged storage roots, and top weight, but no weight reductions occurred at lower inoculum levels. Slight reductions were observed with *M. javanica*, but these were not significant at any inoculation level. Thus, it appears that relatively high *Meloidogyne* populations must be present to result in yield loss in cassava.

Accordingly, control of *Meloidogyne* spp. on cassava may be needed only in certain cases. General methods for nematode management on cassava have been outlined by Dickson (30) and by Hogg (40), in-
cluding use of nematode-free planting stock, crop rotation, disposal of crop residues, flooding, fallowing, use of resistant varieties, and chemical control. Since stem cuttings are used in propagation, contamination of planting material with nematodes ordinarily would not be a problem with cassava, unless the cuttings were somehow permitted to come in contact with heavily infested soil.

Of the various control measures proposed, use of resistant cultivars has received the most emphasis, since many differences in response to root-knot nematodes are evident. Cassava breeding lines have been evaluated at the IITA, but a recent test showed all 56 lines tested to be susceptible to *M. incognita* (race 2) and *M. javanica* (20). Another test showed 8 of 40 breeding lines to be free of galling after 7 months in a field infested with *M. incognita* (4). Seven cassava cultivars were each inoculated with 20,000 eggs of *M. javanica* in a replicated test in Malawi (74) and evaluated after 55 days. ‘Masangwi’ was found to be immune to *M. javanica*, ‘Chithekele’ was highly susceptible, and the other 5 cultivars were intermediate in susceptibility. Kirby (44, 75) tested the reaction of 5 cultivars to 3 root-knot nematode species in Fiji. ‘Merelesita Hybrid’ showed a high level of resistance to *M. arenaria* and moderate resistance to *M. javanica*, ‘Vulatolu’ and ‘Yabia Damu’ showed some degree of resistance to both *M. arenaria* and *M. javanica*, while ‘Bega’ and ‘Sokabale’ were moderately resistant to *M. javanica* but susceptible to *M. arenaria*. All five cultivars were susceptible to *M. incognita*. In Colombia, ‘M. Col. 22’ has shown a high level of resistance to *M. incognita* in a field test in which other cultivars were damaged (2). DaPonte *et al.* (25) evaluated the reaction of 25 cassava cultivars to a mixed population of *M. incognita* and *M. javanica* in a greenhouse test in Brazil, but did not recover *M. javanica* from any cultivar after 60 days, probably because this species comprised a low percentage of the original inoculum. The cultivars ‘Curimanzinha’, ‘Riqueza-IPEACO’, and ‘Saracura’ were susceptible to *M. incognita*, and ‘Do Ceu’, ‘Guarani’, and ‘Olho Roxo’ were considered highly resistant to this species. No *M. incognita* were recovered from the following 19 cultivars, and thus they were considered immune: ‘Aipim Bravo’, ‘Amansa 10’, ‘Amarelona’, ‘Cangaiba’, ‘Catolé’, ‘Ceará’, ‘Cigana’, ‘Cruvela’, ‘Fio de Ouro’, ‘Macacheira de 3 meses’, ‘Macacheira Preta’, ‘Mamão’, ‘Manipeba’, ‘Manirainha’, ‘Manteiga’, ‘Milagrosa’, ‘Para’, ‘Pernambuco’, and ‘Serra Grande’.

Other methods for managing root-knot nematodes on cassava have not been studied as extensively. Fumigation with DBCP has been used to control *M. javanica* in the Ivory Coast (31), but no increase in yield was obtained. In pot experiments with *M. incognita* and *Rotylenchulus reniformis* Linford & Oliveira, DBCP and aldicarb reduced populations by
65-80%, carbofuran and Bunema® by 45-70%, and triazophos was ineffective (37).

There is some evidence that the cassava peel and other by-products may be beneficial in reducing populations of *Meloidogyne* when used as soil amendments (24, 74). However, caution should be used when attempting control by such soil additives because of the risk of introduction of nematodes and pathogens from contaminated crop residues (40). In fact there is evidence that use of crop residues as mulch may actually favor nematode population increases (4).

Caveness (16) points out that nematode populations respond more to cropping systems than to mulching. Crop rotation has been recommended as a control measure (6, 40, 65), and there is evidence that cassava can be used successfully in a rotation with 7 other crops (33). Luc (49) reports that *M. incognita* may not be a serious problem when cassava is grown along with other plants, unless it is intercropped with susceptible hosts such as okra or eggplant. Fallowing may also be useful in reducing root-knot nematode populations, unless the use of agricultural land intensifies to a point where it is no longer a practical option (18). Studies of various cropping systems, including rotation, intercropping, and fallowing, will likely result in specific recommendations that could lower *Meloidogyne* populations below the threshold numbers needed to damage cassava.

*Lesion nematodes (Pratylenchus spp.)*

*Pratylenchus brachyurus* is an important parasite of cassava in many diverse locations, including Togo (28, 49), Nigeria (13), Ivory Coast (31), Madagascar (47, 49), Malaysia (71), Fiji (89), Brazil (21, 82, 90), and Florida (55). Indeed the geographical distribution and host range of this nematode is so great (23) that it is probably present in most cassava-growing regions of the world. Cassava is an excellent host of *P. brachyurus*, with a population increase of 8.43x after 3 months in a greenhouse test using the cultivar ‘IAC-105.66’ (21). The effects of *P. brachyurus* on cassava have been described by deGuiran (28), who observed a gradual decline in production over a period of several years near Ganave, Togo. *P. brachyurus* occurred in high numbers in the soil from this site, along with *Helicotylenchus erythrinae* (Zimmermann) Golden. Seasonal population fluctuations were evident, with the highest observed during November and December, and lowest populations in August, which is the hottest and driest part of the year. *P. brachyurus* was also found in high numbers in the roots, and because of its endoparasitic habits was considered more pathogenic than *H. erythrinae* (28, 49). Fumigation of the site with 50 L/ha of DBCP resulted in a significant (P = 0.05) increase
of 7.9% in total plant weight (tops and enlarged roots) in the fumigated plots compared to untreated controls (28, 57).

DeGuiran (28) also tested the susceptibility of 42 cassava cultivars by inoculating each with 2500 females of P. brachyurus. After 3 months, 7 cultivars had less than 500 P. brachyurus per 100 g of roots, with ‘B25x50’ the lowest at 63/100 g. ‘Touye’ was the most susceptible cultivar, with 14,000/100 g. Such differences suggest that use of tolerant or resistant cultivars could be a possible control measure (23, 28, 45). Crop rotation may also be useful in reducing P. brachyurus if a cover crop of low susceptibility, such as Stylosanthes gracilis, is used (28), but maize should be avoided (57).

Other lesion nematodes found in association with cassava are P. coffeae (Zimmermann) Filipjef & Schuurmans Stekhoven in Java (27), P. zeae Graham in the Philippines (84), and P. sefaensis in Nigeria (4). Pratylenchus species have also been reported from the crop in Nigeria (13), Malawi-Zambia-Zimbabwe (53), Taiwan (42), Fiji (5), Dominican Republic (80), and Trinidad (11).

Reniform nematodes (Rotylenchus spp.)

Cassava is a host of Rotylenchulus reniformis, although it is not as good a host as a number of other tropical crops examined in Ghana (67, 68). In an inoculation test with 15,000 R. reniformis per pot (4), no nematodes were recovered after one year and no measurable effects on plant growth occurred, although reductions did occur in the same test when Meloidogyne spp. were used as inoculum. R. reniformis is widely distributed on cassava, and has been reported from Nigeria (4, 13), Togo (28), Florida (54, 55), Jamaica (45), Trinidad (11), Philippines (37), and in 58% of the cassava samples in a survey conducted in Fiji (89). Rotylenchulus species have been reported on the crop from Puerto Rico (8), the French West Indies (77), Nigeria (45), Malawi-Zambia-Zimbabwe (53), Taiwan (42), Philippines (35), and Fiji (5). Despite their frequent occurrence, no economic damage has been attributed to reniform nematodes on cassava.

Spiral nematodes and other Hoplolaimidae

Many species of spiral nematodes have been found associated with cassava. Helicotylenchus cavenessi Sher was described from soil around cassava roots in Nigeria (78), and other species found in Nigeria have included H. dihystera (Cobb) Sher (13), H. erythrinae (13), H. longicaudatus Sher (78), H. microcephalus Sher (78), H. multicinctus (Cobb) Golden (13), and H. pseudorobustus (Steiner) Golden (14). The widely
distributed *H. dihystera* also has been reported from Florida (54,55), Brazil (90), and Fiji (89). *H. erythrinae* was found in Togo in the same area damaged by *P. brachyurus* (28), *H. microcephalus* has also been found in Fiji (89), and *H. concavus* Roman was found in the Philippines (84). Unidentified species of *Helicotylenchus* are reported from Nigeria (13), Togo (50), Philippines (35), Taiwan (42), Fiji (5), Colombia (2), Dominican Republic (80), and Trinidad (11).

*Scutellonema* spp. are also common on cassava in Africa. *S. aberrans* (Whitehead) Sher and *S. brady* (Steiner & Le Hew) Andrassy are reported from Nigeria (13) and Togo (28, 50). *S. cavenessi* Sher and a *Scutellonema* species are reported from Nigeria (13), and *S. clathricaudatum* Whitehead from Nigeria (14) and Zaire (1).

Other Hoplolaimidae reported occurring on cassava are *Hoplolaimus pararobustus* (Schuermans Stekhoven & Teunissen) Sher and *Peltamigratus nigeriensis* Sher from Nigeria (13, 14). *Hoplolaimus* sp. is reported from Fiji (5) and *Rotylenchus* sp. from Honduras (69).

Hoplolaimidae can be found in high numbers around the roots of cassava plants. In a shadehouse test (14), cassava was found to be an excellent host of *S. clathricaudatum* and *H. microcephalus*, a moderate host of *H. pseudorobustus* and *H. cavenessi*, but a poor host of *P. nigeriensis*. Despite the suitability of cassava as a host for Hoplolaimidae, they are not considered a detriment to crop productivity (28, 49). Populations of *H. dihystera* as great as 700 to 1000/100 cm³ of soil have been observed around cassava roots, without any symptoms of damage to the plant (54, 55).

Other plant-parasitic nematodes reported to be associated with cassava are summarized in Table 1. No economic damage to cassava has been attributed to any of them. Some of them, e.g., *Aphelenchus avenae* Bastian, are more often encountered as fungal feeders, and their association with cassava roots may be as part of the decomposition process. Other microbotrophic nematodes associated with cassava roots are mentioned by other authors (38, 70). Nematode parasites of other *Manihot* species are mentioned by Goodey *et al.* (39).

**Field studies in Florida**

Cassava has been cultivated in Florida since the 1860's (85), and was once used as a commercial source of starch (58). Today, in addition to food production, cassava has potential as a biofuel crop in Florida (63) with fresh root yields approaching 30 mt/ha/annum (64). Recognized damage to cassava in Florida by root-knot nematodes dates back to Neal's observation in 1889 (59).

Because of the importance of root-knot nematodes on cassava, two
Table 1. Miscellaneous plant-parasitic nematodes reported from cassava by geographical region.

<table>
<thead>
<tr>
<th>Nematode</th>
<th>Geographical location and reference</th>
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<tbody>
<tr>
<td><em>Anguina</em> sp.</td>
<td>Malawi-Zambia-Zimbabwe (53)</td>
</tr>
<tr>
<td><em>Aphelenchoides</em> spp.</td>
<td>Brazil (41), Malawi-Zambia-Zimbabwe (53), Taiwan (42)</td>
</tr>
<tr>
<td><em>Aphelenchus avenae</em> Bastian</td>
<td>Brazil (41), Togo (50)</td>
</tr>
<tr>
<td><em>Aphelenchus</em> spp.</td>
<td>Malawi-Zambia-Zimbabwe (53), Taiwan (42), Trinidad (11)</td>
</tr>
<tr>
<td><em>Belonolaimus lineatus</em> Roman</td>
<td>Puerto Rico (73)</td>
</tr>
<tr>
<td><em>Criconemella citri</em> (Steiner) Luc &amp; Raski</td>
<td>Madagascar (47, 48), Togo (28)</td>
</tr>
<tr>
<td><em>C. denoudeni</em> (de Grisse) Luc &amp; Raski</td>
<td>Fiji (89)</td>
</tr>
<tr>
<td><em>C. onoensis</em> (Luc) Luc &amp; Raski</td>
<td>Fiji (89)</td>
</tr>
<tr>
<td><em>C. sphaerocrephala</em> (Taylor) Luc &amp; Raski</td>
<td>Togo (50, 88)</td>
</tr>
<tr>
<td><em>C. tescorum</em> (de Guiran) Luc &amp; Raski</td>
<td>Togo (46)</td>
</tr>
<tr>
<td><em>Criconemella</em> spp.</td>
<td>Malawi-Zambia-Zimbabwe (53), Nigeria (13), Togo (28), Trinidad (11)</td>
</tr>
<tr>
<td><em>Ditylenchus dipsaci</em> (Kuhn) Filipjev</td>
<td>Brazil (70), Unknown (81)</td>
</tr>
<tr>
<td><em>Ditylenchus</em> spp.</td>
<td>Malawi-Zambia-Zimbabwe (53), Taiwan (42)</td>
</tr>
<tr>
<td><em>Hemicriconemoides cocophilus</em> (Loos)</td>
<td>Nigeria (13)</td>
</tr>
<tr>
<td>Chitwood &amp; Birchfield</td>
<td></td>
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<tr>
<td><em>Hemicriconemoides</em> spp.</td>
<td></td>
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<tr>
<td><em>Hemicyciophora oostenbrinki</em> Luc</td>
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<tr>
<td><em>H. penetrans</em> Thorne</td>
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<tr>
<td><em>Hemicycliciophora</em> sp.</td>
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<tr>
<td><em>Heterodera</em> sp.</td>
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<tr>
<td><em>Paratylenchus</em> sp.</td>
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<tr>
<td><em>Radopholus</em> spp.</td>
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<tr>
<td><em>Tetylenchus</em> sp.</td>
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<tr>
<td><em>Trichodorus</em> spp.</td>
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Table 1. Miscellaneous plant-parasitic nematodes reported from cassava by geographical region. (Continued).

<table>
<thead>
<tr>
<th>Nematode</th>
<th>Geographical location and reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tylenchoryzhus triglyphus</em> Seinhorst</td>
<td>Philippines (84)</td>
</tr>
<tr>
<td><em>Tylenchorhynchos</em> sp.</td>
<td>Taiwan (42)</td>
</tr>
<tr>
<td><em>Tylenchulus</em> sp.</td>
<td>Taiwan (42)</td>
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<tr>
<td><em>Tylenchus</em> spp.</td>
<td>Malawi-Zambia-Zimbabwe (53), Taiwan (42), Togo (28), Trinidad (11)</td>
</tr>
<tr>
<td><em>Xiphinema ebriense</em> Luc</td>
<td>Nigeria (13)</td>
</tr>
<tr>
<td><em>X. elongatum</em> Schuurmans Stekhoven &amp; Teunissen</td>
<td>Philippines (84), Togo (28)</td>
</tr>
<tr>
<td><em>X. ijacolum</em> Luc</td>
<td>Nigeria (13)</td>
</tr>
<tr>
<td><em>X. longicaudatus</em> Luc</td>
<td>Nigeria (13)</td>
</tr>
<tr>
<td><em>X. nigeriense</em> Luc</td>
<td>Nigeria (13)</td>
</tr>
<tr>
<td><em>X. rotundatum</em> Schuurmans Stekhoven &amp; Teunissen</td>
<td>Nigeria (13)</td>
</tr>
<tr>
<td><em>X. setariae</em> Luc</td>
<td>Nigeria (13)</td>
</tr>
<tr>
<td><em>Xiphinema</em> spp.</td>
<td>Brazil (41), Colombia (2), Fiji (5), Malawi-Zambia-Zimbabwe (53)</td>
</tr>
</tbody>
</table>

tests were conducted in southern Florida in 1982 to examine the effects of *M. incognita* on the crop in this region as well as some possible control measures. In one test, the damage from this nematode was observed throughout a growing season and relationships developed between nematode levels and various plant parameters. In a second field experiment, yields of four cassava cultivars were compared in fumigated and unfumigated plots.

**MATERIALS AND METHODS**

*M. incognita Observation Plot.* This plot was located on a Rockdale fine sandy loam soil approximately 18 km north of Homestead, Florida, and was planted to the cassava cultivar ‘Senorita’ in February, 1982. Cuttings were planted horizontally about 5 cm deep, at a spacing of approximately 1.0 m. On May 19, 25 single-stemmed plants were selected at random and harvested from a 1.0 ha area of the field. The following plant parameters were determined for each of the 25 plants: stem height
and diameter at ground level, fresh weight and diameter of the original cutting, fresh top weight, number and fresh weight of enlarged roots, and fresh weight of small, fibrous roots (Fig. 1). The number of *M. incognita* egg masses per root system were counted for each plant. This procedure was repeated at harvest on November 4, except that the number and fresh weight of enlarged roots were further broken down into marketable roots and culls. Correlations between the various parameters were then determined for each sampling date.

*Cassava Cultivar Evaluation.* Four cassava cultivars were examined in this experiment: the common local cultivar, ‘Senorita’, and three introductions from CIAT in Cali, Colombia, namely ‘HMC-2’, ‘CMC-92’, and ‘Mantiqueira’ (CMC-40), the last of which had been previously described from Brazil (76). These were selected for inclusion in the test based

![Fig. 1. Schematic diagram of cassava root system.](image-url)
on their performance in agroecosystems similar to those of southern Florida. Experimental plots were established on raised beds of Rockdale fine sandy loam soil (pH = 7.6) at the Agricultural Research and Education Center in Homestead, Florida. The experimental design was a split plot with soil fumigation treatments as the main plots and cultivars as subplots. The design was replicated six times. Prior to fumigation, pendimethalin (2.34 liters/ha) was applied to the site and fertilizer (7-14-14) was incorporated into the beds at a rate of 448 kg/ha. On May 18, 1982, 58.9 liters ai/ha of ethylene dibromide (65.4 L/ha of Soilbrom® 90EC) were applied to one-half of the experimental plots. The fumigant was injected into the soil at a depth of 12-15 cm through three chisels spaced 0.3 m apart. All beds, fumigated or unfumigated, were then covered by a thin opaque plastic mulch until May 21, 1982. Cuttings of the four cassava cultivars were planted in a vertical position on May 28. Four cuttings per cultivar were spaced 1.0 m apart in rows (main plots) which were 1.8 m apart. Weed control in all plots was maintained by applications of paraquat. Since disease and insect problems did not develop, no other pesticides were used. On July 19, 67 g of fertilizer (7-14-14) were lightly incorporated around each plant.

Soil samples for assay of plant-parasitic nematodes were collected on May 25 and December 14, 1982. Each sample consisted of soil collected with a hand trowel to a depth of 15 cm from three locations around each of the four plants per subplot. Each soil sample was passed through a 4.0 mm sieve to remove rock, and a 100 cm³ subsample was processed for nematodes by a modified sieving and centrifugation procedure (43, 54).

On December 20, 1982, the stems and leaves were harvested from two plants per subplot and weighed. A subsample of 500-1000 g from each was dried at 80°C to determine percent dry weight. Roots from all plants in each subplot were separated into marketable enlarged roots and other root material, mostly enlarged roots that had been culled for small size. A subsample of approximately 300 g was taken from the proximal, central, and distal sections of two marketable enlarged roots per subplot and oven-dried to determine percent dry root weight. The number of egg masses from M. incognita was determined for each root system. Since less than 100% of the 'CMC-92' cuttings survived, the actual number of plants per subplot was counted and all data converted to yield per plant. Nematode and harvest data were analyzed by an analysis of variance (ANOVA) for a split-plot design, followed by Duncan's new multiple range test for those cases in which a mean separation test was appropriate. Prior to analysis, nematode data were transformed by \[ \log_{10} (x + 1) \] and percentage data by arcsine (\(\sqrt{x}\)).
RESULTS AND DISCUSSION

*M. incognita* Observation Plot. During the course of the growing season, a heavy infestation of *M. incognita* developed in this field. By the May 19 sampling, when the plants were 3 months old, plants in some parts of the field were exhibiting stunting and chlorosis. Top weight was negatively correlated with the number of *M. incognita* egg masses per gram of fibrous root material, with \( r = -0.395 \), but this was not significant, since weight of the vegetative cutting or "seedpiece" appeared to be more strongly correlated with top weight at this stage of growth (Table 2). Storage roots were just beginning to enlarge at this time, and did not show any relationship to root-knot nematode levels or weight of the vegetative cuttings.

By harvest (9 mos. after planting), many significant relationships were apparent between weights of various plant parts and root-knot nematode levels (Table 2). Since most plant parameters were significantly \( (P = 0.01) \) correlated with one another (e.g., plant height vs. top weight), only relationships involving top weight, marketable root weight, and total root weight are presented (Table 2). In addition, many plant parameters showed significant \( (P = 0.05) \) negative correlations with total number of galls per root system or with various logarithmic transformations of that quantity. However, the corresponding correlations with egg masses per gram of fibrous root tissue were always greatest (highest \( r^2 \)). Because of its size, a large, vigorous root system may contain many egg masses, but a density measurement, such as egg masses per gram, may be more meaningful in terms of plant growth response. All plant parameters measured at harvest (Table 2) had negative linear correlations with *M. incognita* per gram and positive linear correlations with the seedpiece weight. Because *M. incognita* density and seedpiece weight had opposite effects, the multiple regression models were better predictors of the various plant yield measurements, as shown by the greater \( R^2 \) values.

The opposite effects of number of egg masses per gram of fibrous roots and cutting weight on total weight of the enlarged roots are illustrated (Fig. 2). Since each data point represents a single plant, the weight of enlarged roots per plant is highly variable. Yet marketable yield is clearly reduced with high nematode density and lighter cuttings, and is greatest with heavier cuttings and low nematode density. Yields dropped dramatically with nematode densities of more than 10-15 egg masses per gram of fresh fibrous root weight, or 210-320 egg masses per root system, based on a mean of 21 g fresh fibrous roots per plant. At low densities, i.e. less than 10 egg masses per gram, interpretation of yield relationships is difficult, due to the effect of vegetative cutting
Table 2. Coefficients of determination ($r^2$, $R^2$) between various plant yield parameters and independent variables influencing yield, including weight of the original vegetative cutting and/or galls per gram of root on two sampling dates in 1982.

<table>
<thead>
<tr>
<th>Dependent variable (yields in g)</th>
<th>Independent variable$^w$</th>
<th>MI$^z$ (linear $r^2$)</th>
<th>SW* (linear $r^2$)</th>
<th>MI, SW (multiple $R^2$)</th>
<th>Multiple regression equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fresh top weight (TOP)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>May 19</td>
</tr>
<tr>
<td>Total root weight (TR)$^z$</td>
<td></td>
<td>0.156</td>
<td>0.683***</td>
<td>0.690***</td>
<td></td>
</tr>
<tr>
<td>Fresh top weight (TOP)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>November 4</td>
</tr>
<tr>
<td>Marketable root weight (MR)</td>
<td></td>
<td>0.262**</td>
<td>0.498***</td>
<td>0.577***</td>
<td>TOP = 2.64 + 4.42SW — 10.9MI</td>
</tr>
<tr>
<td>Total root weight (TR)$^z$</td>
<td></td>
<td>0.321**</td>
<td>0.128</td>
<td>0.349**</td>
<td>MR = 709 + 1.47SW — 20.3MI</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.424***</td>
<td>0.196*</td>
<td>0.476***</td>
<td>TR = 980 + 2.36SW — 2.72MI</td>
</tr>
</tbody>
</table>

$^w$Asterisks ( *, **, *** ) indicate significant relationships at $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.

$^z$MI = *M. incognita* egg masses per gram of fresh fibrous root material.

$^y$SW = Fresh weight of the cassava “seedpiece” in grams.

$^z$All enlarged roots, including culls.
Fig. 2. Three-dimensional relationship between total root weight, egg masses per gram of fibrous roots, and fresh weight of the vegetative cutting.

weight, but it is likely that the plants may have some tolerance of low \textit{M. incognita} levels.

Despite very high levels of \textit{M. incognita} on some plants, no galling or egg masses were observed on any of the enlarged roots at harvest, nor
were any roots culled because of direct damage or distortion attributed to the nematodes. The effects of *M. incognita* on cassava are probably indirect, with infected plants not being able to produce large marketable roots. As early as August 6 (6 mos. after planting), the dramatic effects of root-knot nematodes in minimizing enlarged root development were evident (Fig. 3). Plants heavily infected with *M. incognita* had no enlarged roots by this date, but several large roots had formed on plants which did not exhibit such a high level of galling. The roots which should have enlarged can be identified from Fig. 3, yet are heavily galled and show no enlargement. It is possible that the enlargement of cassava roots can be prevented by an early-season, heavy penetration by root-knot nematodes. At harvest (9 mos. after planting), there was a highly significant (*P* = 0.01) negative correlation between number of enlarged roots per plant and number of egg masses per gram of fibrous roots, with *r* = —0.654.

*Cassava Cultivar Evaluation.* There were no significant (*P* = 0.05) treatment effects or interactions observed for the yield parameters measured in this test (Table 3). However, subplot (cultivar) effects were significant, and so the values for each cultivar are averaged across treat-

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**Fig. 3.** Photo of *M. incognita* damage to 6-month-old ‘Senorita’ cassava root system, showing original cutting used as a “seedpiece” (A), site of the plant stem (B), a large root that should have enlarged into a storage root (C), and galls from *M. incognita* on fibrous roots (D).
Fig. 3. Photo of *M. incognita* damage to 6-month-old ‘Senorita’ cassava root system, showing original cutting used as a “seedpiece” (A), site of the plant stem (B), a large root that should have enlarged into a storage root (C), and galls from *M. incognita* on fibrous roots (D).
Table 3. Harvest weights per plant by cassava cultivar, December 20, 1982.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Number of marketable roots</th>
<th>Dry weight in kg of:</th>
<th>Percentage of total plant dry weight of:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Marketable roots</td>
<td>Total root material</td>
</tr>
<tr>
<td>Mantiqueira</td>
<td>4.94 a</td>
<td>1.17 a</td>
<td>1.35 a</td>
</tr>
<tr>
<td>Senorita</td>
<td>3.93 b</td>
<td>0.98 ab</td>
<td>1.25 a</td>
</tr>
<tr>
<td>HMC-2</td>
<td>3.66 b</td>
<td>0.88 b</td>
<td>1.24 a</td>
</tr>
<tr>
<td>CMC-92</td>
<td>2.56 c</td>
<td>0.48 c</td>
<td>0.86 b</td>
</tr>
</tbody>
</table>

*Data are means of two treatments x six replications since no significant main (treatment) effects existed for these measurements. Means in columns followed by the same letter are not significantly (P = 0.05) different, according to Duncan's new multiple range test.
ment type. 'Mantiqueira' and 'Senorita' stored 65% and 68% of the total dry matter in the form of root material, respectively. This was significantly greater than 'HMC-2', which stored only 55% of its total dry matter in the roots, or 'CMC-92', which produced more top biomass than root biomass. 'Mantiqueira' produced more marketable roots than 'Senorita', but they were slightly smaller in size, with the result that the total weight of marketable roots per plant was similar for both cultivars. 'CMC-92' was poorly adapted to southern Florida. Its roots appeared to be immature at the harvest date and top growth was excessive in comparison to root yield.

Plant-parasitic nematodes present in the site prior to planting were *Meloidogyne incognita*, *Rotylenchulus reniformis*, *Helicotylenchus dihystera*, *Quinisulcius acutus* (Allen) Siddiqi, and *Criconemella* sp. Lack of significant fumigation treatment effects on yield indicated that nematode populations in the experimental plots were probably subthreshold. The initial population of *M. incognita* juveniles averaged one per 100 cm$^3$ of soil, while initial populations of other species were higher (Table 4). *Helicotylenchus dihystera* maintained its population during the growing season on cassava, but populations of three other species had decreased by the harvest date. One species showing a slight decline under cassava was *R. reniformis*, which is surprising, considering the widespread reports of this nematode on this crop. Although cassava was a suitable host for maintaining *R. reniformis* populations, this crop did not result

Table 4. Initial and final nematode populations by treatment in the cassava cultivar test, 1982.

<table>
<thead>
<tr>
<th>Nematode</th>
<th>Nematodes per 100cm$^3$ of soil</th>
<th>December 14$^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>May 25$^a$</td>
<td>Unfumigated</td>
</tr>
<tr>
<td><em>Helicotylenchus dihystera</em></td>
<td>10.8</td>
<td>16.9</td>
</tr>
<tr>
<td><em>Rotylenchulus reniformis</em></td>
<td>57.5</td>
<td>32.3</td>
</tr>
<tr>
<td><em>Quinisulcius acutus</em></td>
<td>11.7</td>
<td>2.5</td>
</tr>
<tr>
<td><em>Criconemella</em> sp.</td>
<td>3.3</td>
<td>0.2</td>
</tr>
</tbody>
</table>

$^a$Mean of six unfumigated main plots.

$^b$Means of six replications x four cultivars. Counts were averaged across cultivars since no significant subplot effects occurred for these species.

$^c$Asterisks (**, *** ) indicate significant differences from unfumigated control at P = 0.01 and P = 0.001, respectively, for the December 14 data for each species.
in the great population increases of this nematode which the authors have observed for other crops in this region, such as sweetpotato or papaya. This result, along with previous information (4), suggest that cassava is unlikely to be economically damaged by *R. reniformis* and may be only a weak host of the nematode. Some of the species shown in Table 4 were significantly reduced by fumigation, but none were significantly (P = 0.05) influenced by cultivar differences.

Although initial populations of *M. incognita* juveniles in the soil were very low, a bioassay test (56) performed after fumigation, but before planting, revealed an average of 21.8 galls per bioassay plant in unfumigated plots. This was significantly (P = 0.05) more than the zero galls per plant found in fumigated plots. However, considering the lack of significant treatment effects on yield (Table 3), these levels must also be regarded as subthreshold. Final *M. incognita* populations in the experimental plots (Table 5) exhibited significant (P = 0.05) differences by treatment and by cultivar, as well as a significant treatment x cultivar interaction. *M. incognita* populations at harvest in fumigated plots were very low and showed no differences by cultivar, but soil populations in unfumigated plots were very high, particularly on ‘Senorita’ and ‘HMC-2’. Galling on ‘Senorita’ was much greater than on the other cultivars, which developed very low levels of galling even in unfumigated plots. However, in all unfumigated plots, enough *M. incognita* reproduction had occurred to result in substantial increases in final populations of soil juveniles, compared to the initial populations.

While ‘Senorita’ is widely grown in southern Florida, its susceptibility to *M. incognita* and the possibility of damage at high population levels

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Larvae per 100cm³ of soil⁶</th>
<th>Galls per plant⁶</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fumigated</td>
<td>Unfumigated</td>
</tr>
<tr>
<td>Senorita</td>
<td>12.5 n.s.</td>
<td>758 a</td>
</tr>
<tr>
<td>Mantiqueira</td>
<td>9.2</td>
<td>262 b</td>
</tr>
<tr>
<td>HMC-2</td>
<td>10.0</td>
<td>613 a</td>
</tr>
<tr>
<td>CMC-92</td>
<td>11.7</td>
<td>320 b</td>
</tr>
</tbody>
</table>

⁶Means of six replications. Means followed by the same letters are not significantly (P = 0.05) different, according to Duncan’s new multiple range test; n.s. = no significant differences by cultivar.
make it a less desirable choice for optimum cassava production in sites infested by root-knot nematodes. Although no yield losses were apparent on ‘Senorita’ grown in plots with low M. incognita levels (Table 3), significant losses occurred when this cultivar was grown in a site infested by high populations (Table 2). Other cultivars were less susceptible to M. incognita than ‘Senorita’, and ‘Mantiqueira’ equalled ‘Senorita’ in terms of marketable yield, although it produced slightly smaller marketable roots. Further testing of the response of ‘Mantiqueira’ to high nematode populations is needed, but the possibility of lower M. incognita susceptibility as well as some of the other desirable features such as early maturity (6) may enhance the acceptance of this cultivar in southern Florida. Indeed, the variation in response of cassava cultivars to root-knot nematodes worldwide indicates that use of resistance or tolerant cultivars may be the most promising method for managing Meloidogyne spp. on cassava in most regions of the world. Results obtained in this study and by Caveness (17) and by Gapasin (36) emphasize that management would be necessary only under certain conditions, since the threshold of measurable plant damage to cassava by Meloidogyne is relatively great. For comparative purposes, levels of 280-750 juveniles/100 cm³ of soil at harvest were quite damaging in a test in Nigeria (17), but numbers of 262-758/100 cm³ of soil here (Table 5) resulted in no significant losses, presumably because of the differences in climate, cultivars, and Meloidogyne species and populations. To obtain heavy damage, a combination of a high Meloidogyne population and susceptible cassava cultivar would be needed, and it is possible that even ‘Senorita’ may not be nearly as susceptible to damage as some of the African cultivars.

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