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Aggressiveness and Damage Potential of Central American and Caribbean Populations of *Radopholus* spp. in Banana[1]

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Abstract: Monoxenic cultures of burrowing nematode populations extracted from banana roots from Belize, Guatemala, Honduras, and Costa Rica were established on carrot discs. Cultures of *Radopholus* spp. were also obtained from Florida, Puerto Rico, Dominican Republic, and Ivory Coast. The aggressiveness (defined as reproductive fitness and root necrosis) of these populations was evaluated by inoculating banana plants (*Musa* AAA, cv. Grande Naine) with 200 nematodes/plant. Banana plants produced by tissue culture were grown in 0.4-liter styrofoam cups, containing a 1:1 mix of a coarse and a fine sand, at ca. 27 °C and 80% RH. Banana plants were acclimated and allowed to grow for 4 weeks prior to inoculation. Plant height, fresh shoot and root weights, root necrosis, and nematode population densities were determined 8 weeks after inoculation. Burrowing-nematode populations varied in aggressiveness, and their reproductive fitness was generally related to damage reported in the field. Plant height and fresh shoot and root weight did not reflect damage caused by nematodes under our experimental conditions. Necrosis of primary roots was closely related to the reproductive fitness of the nematode populations. Variation in aggressiveness among nematode populations followed a similar trend in the two susceptible hosts tested, Grande Naine and Pisang mas. All nematode populations had a low reproductive factor (Rf $\leq$ 2.5) in the resistant host except for the Ivory Coast population which had a moderate reproductive factor (Rf = 5) on Pisang Jari Buaya. This is the first report of a burrowing nematode population parasitizing this important source of resistance to *R. similis*.

Key words: banana, burrowing nematode, host resistance, *Musa* spp., nematode, *Radopholus,* reproductive fitness.

The burrowing nematode, *Radopholus similis* (Cobb) Thorne, is a migratory endoparasite that is present in many tropical and subtropical regions throughout the world (Kaplan, 1994). It is the most damaging and widespread nematode attacking banana (Gowen and Quénéhervé, 1990; Stover and Simmonds, 1987). Plant-parasitic nematodes cause severe crop losses in commercial Cavendish banana plantations and limit the productivity of non-export dessert and cooking banana (Gowen, 1995; Gowen and Quénéhervé, 1990; Sarah, 1989; Stover and Simmonds, 1987). The extent of nematode damage is variable and is influenced by cultivar, edaphic factors, and the relative aggressiveness of nematode populations (Gowen, 1995; Kaplan and Gottwald, 1992). Estimated yield losses due to nematode damage in banana average 19.7% worldwide (Sasser and Freckman, 1987); however, losses of 14.3–60.5% in the Philippines (Davide, 1994), 50% in Mexico and Puerto Rico (Román, 1986), and 75–80% in South Africa (Sarah, 1989) have been reported.

Successful control of nematodes in established banana plantations relies on the use of organophosphate and carbamate nematicides in combination with agronomic practices, mainly propping or guying of fruit-bearing plants (Gowen, 1994; Gowen and Quénéhervé, 1990; Stover and Simmonds, 1987). Agronomically acceptable resistant cultivators of banana and plantain have been difficult to obtain because of the genetic complexity of *Musa* (Pinochet, 1988a).

Populations of *R. similis* from Latin America, the Caribbean islands, Africa, and Asia vary in their aggressiveness (damage potential and (or) reproductive fitness) (Fallas et al., 1995; Hahn et al., 1994, 1995, 1996;

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Pinochet, 1988b; Sarah and Fallas, 1996; Sarah et al., 1993; Tarté et al., 1981). Recent investigations have focused on characterizing the variability in populations from Africa (Fallas et al., 1995; Hahn et al., 1996) and southeast Asia (Hahn et al., 1994); however, there are no recent detailed studies on the genetic variability of burrowing nematode populations from Latin America and the Caribbean. Pinochet (1979) found that more aggressive populations predominate in the southern portion of Central America. Similarly, Tarté et al. (1981) showed that populations from Panama and Costa Rica had higher reproductive rates than those from Honduras or Ecuador. Quantitative assessment of this variability would be useful in banana breeding and research programs in the development of new strategies or tactics for the management of this nematode (Ferrar et al., 1994; Pinochet, 1988b; Rivas and Román, 1985).

Problems have arisen in adapting terminology initially established for other plant parasites or pathogens to nematodes because most stylet-bearing nematodes are primarily parasitic and secondarily pathogenic (Shaner et al., 1992; Triantaphyllou, 1987). In this paper, pathogenicity is considered a qualitative trait and is defined as the capability of the nematode to cause disease. Our study focused on aggressiveness, which reflects a quantitative or relative measure of the general damage potential of a given nematode without regard to resistance genes (Shaner et al., 1992). Thus, for the burrowing nematode-banana pathosystem, we describe aggressiveness by reproductive fitness (Rf) and root necrosis (damage potential). We used both of these parameters because reproductive fitness of the nematode and the amount of damage that it causes to the host may not always be related. In some pathosystems, these attributes are under control of different genes (Shaner et al., 1992). Hahn et al. (1996) found that reproductive fitness of burrowing nematode populations is not necessarily associated with significant damage on banana.

The objectives of this research were to determine the variation in aggressiveness of burrowing nematode populations from Latin America and the Caribbean on banana (*Musa* AAA, Cavendish subgroup, cv. Grande Naine) and to evaluate the interactions of seven nematode populations and three banana genotypes.

Materials and Methods

Aggressiveness tests: Monoxenic cultures of burrowing nematodes from different banana-growing areas of Central America (Table 1) were established on carrot disks (O'Bannon and Taylor, 1968). Selection of sampling sites was based on reported aggressiveness or damage to the crop under field conditions. Root samples from Belize, Guatemala, Honduras, and Costa Rica were used. Established burrowing nematode cultures also were obtained from Florida, Puerto Rico, the Dominican Republic, and

Table 1. Burrowing nematode populations from Latin America, the Caribbean, and Africa.

Population code	Nematode population source[a]	Origin	Host
DK8	DK8	Florida	Citrus[b]
DK7	DK7	Florida	Banana
B	OP810	Stann Creek, Belize	Banana
G1	OP807	Yuma Farm, Guatemala	Banana
G2	OP808	Creek Farm, Guatemala	Banana
G3	OP809	Lanquin Farm, Guatemala	Banana
H1	OP805	Santa Rosa Farm, Honduras	Banana
H2	OP806	Coyoles, Honduras	Banana
CR1	OP801	Balatana Farm, Costa Rica	Banana
CR3	OP803	PAIS Farm, Costa Rica	Banana
CR5	OP804	La Rita Farm, Costa Rica	Banana
PR	DK13	Puerto Rico	Banana
DR	DK15	Dominican Republic	Anthurium
IC	na[c]	Anguededou, Ivory Coast	Banana

[a] Nematode source designations given according to Bird and Riddle (1994).
[b] *Radopholus citrophilus.*
[c] No code assigned.

Ivory Coast. One of the populations from Florida (*R. citrophilus* Huettel, Dickson & Kaplan) and the population from the Dominican Republic were established from nematodes extracted from hosts other than banana (*Citrus* sp. and *Anthurium* sp., respectively). The Ivory Coast population was included as a standard because it had been reported as the most aggressive population tested on banana (Sarah et al., 1993) at the time our study was initiated.

A standardized method was developed to conduct aggressiveness tests in the greenhouse (Marin, 1997). Banana plants (*Musa* AAA, Cavendish Subgroup, cv. Grande Naine) from tissue culture were grown in 0.4-liter styrofoam cups. A 1:1 mixture of sterile, coarse river sand and a 212-µm-diam. quartz sand (Whitehead Brothers, Florham Park, NJ) was used as planting medium. A complete nutrient solution (Chem Gro, Hydro-Gardens, Colorado Springs, CO), based on 100 mg/liter N, was added twice a week, and deionized water was added as needed. The same amount of fertilizer and water was added to all treatments. Plants were acclimated and allowed to grow for 4 weeks at 27 °C and 80% RH in the greenhouse before nematode inoculation. This procedure was previously found to be a reliable measure of relative nematode reproduction per nematode-cultivar combination, and results were comparable to those observed in the field (Marin, 1997).

Burrowing nematodes extracted from excised carrot-disk culture (Kaplan and Davis, 1990) were quantified, concentrated, and resuspended in sterile, deionized water (ca. 40 nematodes/ml). Five ml of the nematode suspension (juveniles plus adults, ca. 200 specimens) was added to the base of each plant and covered with sand. A mixture of juveniles and adults was used. Inoculated plants were maintained for an additional 8 weeks at 27 °C and 80% RH in the greenhouse.

Before harvesting the plants, plant height was measured from the base of the plant to the insertion of the ''cigar'' leaf (the apical unfolded leaf). At harvest, fresh shoot and root weights were recorded, and percent total root necrosis and primary-order root necrosis were estimated visually.

After harvest, roots were cut in 1-cm pieces, and nematodes were extracted with jar incubation at 25 °C for 7 days (Kaplan, 1994). Nematodes were collected on a 25-µm-pore sieve (500-mesh). Nematodes were resuspended in 100 ml of water, and a 10-ml aliquot was taken for quantification of each sample. The final number of nematodes per plant (Pf) reproductive factor (Pf/Pi) and nematodes per gram of root were determined and used as a measure of reproductive fitness.

The experiment was designed and analyzed as a randomized complete block design with 10 replicates, and was repeated once over time. All data were subjected to analysis of variance; nematode data were transformed, with $\log_{10}(x + 1)$ before analyses. Statistical analyses were performed using SAS (release 6.11, SAS Institute Inc., Cary, NC). Means were separated with the Waller-Duncan k-ratio *t*-test.

Host × nematode population interaction: The aggressiveness of seven nematode populations (H1, H2, G2, G3, CR1, CR5, and IC) was assessed on three different banana hosts. Two susceptible banana genotypes (*Musa* AA cultivars Grande Naine and *Musa* AA Pisang mas) and a resistant genotype, (*Musa* AA Pisang Jari Buaya, accession III-106) were used. Experimental procedures were the same as previously described. This experiment was also designed and analyzed as a randomized complete block design with 10 replicates. Nematode data and root necrosis were transformed using $\log_{10}(x + 1)$ and square root of (x), respectively, prior to statistical analyses. Statistical analyses were performed with SAS (SAS Institute Inc., Cary, NC). Means were separated with the Waller-Duncan k-ratio *t*-test.

Results

Aggressiveness tests: Reproductive fitness varied among populations from Central America and the Caribbean islands (Fig. 1). Populations from Costa Rica (CR1) and Guatemala (G3) had the highest reproduc-

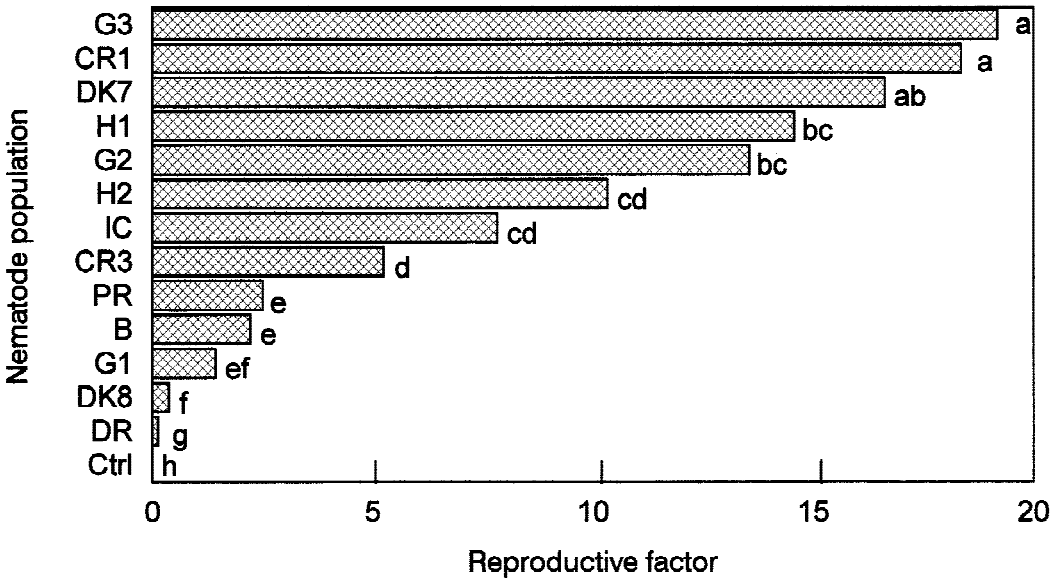

FIG. 1. Reproductive factors of *Radopholus* spp. on banana cv. Grande Naine roots 8 weeks after inoculation. Reproductive factor = final population/initial population. Bars followed by a common letter are not different according to the Waller-Duncan *k*-ratio ($k = 100$) *t*-test. Ctrl: uninoculated control.

tive factors of all populations tested. Reproduction of the population from the Sula Valley (H1) was greater than that from the Coyoles area (H2). Although they were not statistically different, populations G2, IC, and CR3 had an intermediate position in the range of reproductive fitness observed. The populations from Puerto Rico (PR), Belize (B), and Guatemala (G1) had low reproductive factors. The Rfs of the two populations collected from hosts other than banana (DK8 and DR) were significantly lower than Rfs of all populations from banana.

Nematode population density (number of individuals per gram of root) followed the same trend described for the Rf (Fig. 2); high Rf values corresponded to high nematode population densities. Higher *R. similis* numbers were obtained with populations CR1, DK7, and H1. The lowest numbers of nematodes per gram of root were obtained with DK8 and DR, which originated from non-banana hosts.

Significant differences among populations were observed with all plant-growth variables. Plant height was greater with DK7 and DK8 populations than with any other population or the control (Table 2). Plant height was suppressed by populations CR1, CR3, and G2. The non-inoculated control did not produce the tallest plants in the experiment.

Shoot weight was greatest in the non-inoculated control, but it did not differ from plants inoculated with DK8, DK7, IC, B, and G3 (Table 2). Although inoculation with nematode populations CR3, DR, and CR1 resulted in the lightest shoots, their weights were not statistically different from those inoculated with most other populations.

Root weight (Table 2) differed among treatments. Plants inoculated with DR, G3, B, and the control had the heaviest root systems, whereas CR1, G2, and H2 significantly restricted root development. Root necrosis was a better indicator of variation in reproduction than root weight. Total root necrosis (Fig. 3A) differed greatly, with DK7, CR1, and G3 causing the most necrosis. Significantly less damage to the root system was observed with DK8 and DR populations, which did not differ from the non-inoculated control. Non-inoculated control plants also showed about 20% of root necrosis. When only primary-root necrosis was considered, the necrosis in the control was

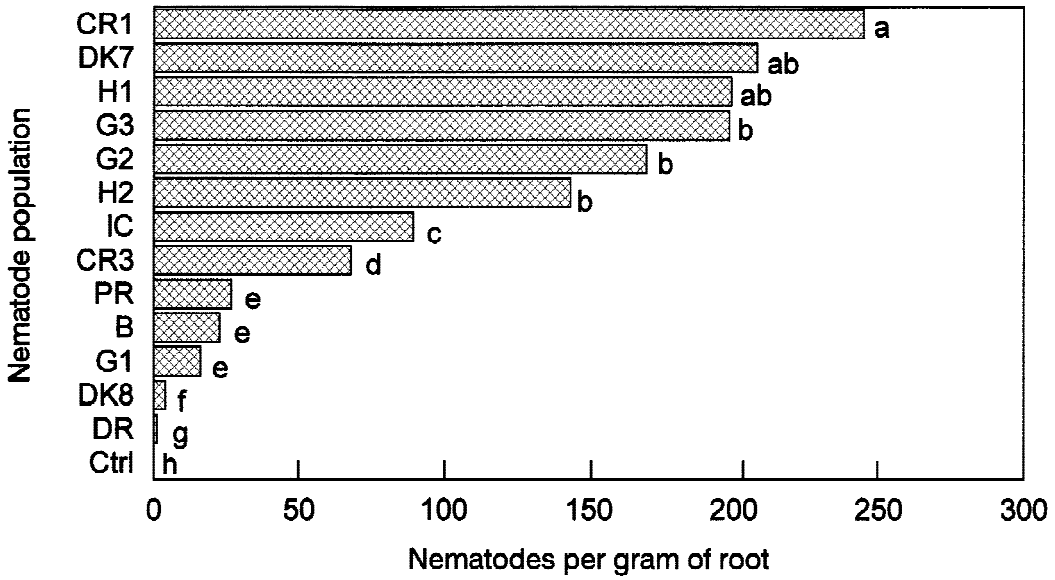

FIG. 2. Reproduction of 13 populations of *Radopholus* spp. on a nematode-per-gram basis on banana cv. Grande Naine roots 8 weeks after inoculation. Bars followed by a common letter are not different according to the Waller-Duncan *k*-ratio ($k = 100$) *t*-test. Ctrl: uninoculated control.

only about 5% (Fig. 3B). Total root necrosis and primary root necrosis were closely related when the values were high. However, primary-root necrosis was significantly less than total-necrosis for less damaging populations such as DK8 and DR.

Reproductive fitness (Rf) was better correlated with total root necrosis ($r = 0.77$, $P < 0.001$) and primary-root necrosis ($r = 0.79$, $P < 0.001$) than with plant height ($r = 0.27$, $P = 0.002$), fresh shoot ($r = 0.04$, $P = 0.689$), and root weight ($r = -0.43$, $P < 0.001$).

Host × nematode population interaction: A significant interaction between nematode populations and banana genotypes was observed. Therefore, statistical analyses were performed individually for each genotype. Variation in reproductive factors followed a similar trend in the two susceptible hosts, Grande Naine and Pisang mas (Fig. 4). Nematode populations IC and CR5 showed the highest Rf in Grande Naine, followed by CR1, G2, and H2. The nematode population from the Sula Valley (H1) had a lower Rf than the other populations tested. In Pisang mas, CR1 did not differ significantly from IC and CR5, the most aggressive populations tested. H1 had the lowest Rf in Pisang mas and Grande Naine. All populations but IC exhibited a low Rf in Pisang Jari Buaya (Fig. 4). IC reproduced well in Pisang Jari Buaya (Rf = 15), although less than the most aggressive populations in the susceptible hosts. The citrus populations [*R. citrophilus* (DK8)] did not reproduce on bananas.

Primary-root necrosis (Fig. 5) was closely related to the Rf for the susceptible hosts.

TABLE 2. Effects of 11 populations of *Radopholus* spp. on growth of susceptible banana (Grande Naine).

Nematode population[a]	Plant height (cm)	Shoot weight (g)	Root weight (g)
DK7	13.6 a[b]	21.2 ab	18.1 bcd
DK8	13.4 a	21.4 a	19.2 abc
IC	12.8 b	21.2 ab	18.8 abcd
PR	12.8 b	19.4 cd	18.5 abcd
DR	12.7 b	18.9 d	20.4 a
G3	12.7 b	20.2 abcd	20.3 a
B	12.6 bc	20.7 abc	20.0 ab
H2	12.5 bc	19.8 bcd	15.6 e
Control	12.5 b	21.6 a	19.8 ab
CR1	12.3 bcd	18.7 d	17.0 cde
CR3	12.1 cd	18.9 d	18.3 abcd
G2	11.9 d	19.5 cd	16.6 de

[a] See Table 1 for description of nematode populations. Control = uninoculated plant.

[b] Numbers followed by the same letter in a column are not different according to the Waller-Duncan *k*-ratio ($k = 100$) *t*-test.

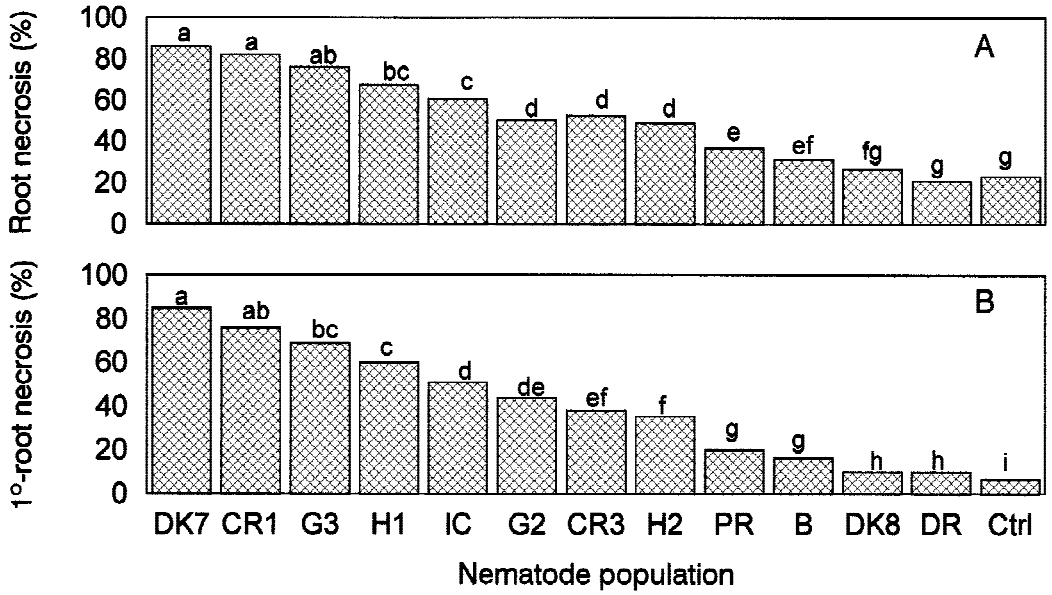

FIG. 3. Association of root necrosis of banana cv. Grande Naine with 12 populations of *Radopholus* spp. 8 weeks after inoculation. A) Total necrosis. B) Primary (1°) necrosis. Bars with a common letter are not different according to the Waller-Duncan *k*-ratio ($k = 100$) *t*-test. Ctrl: uninoculated control.

Although the Rf of the CR1 population was less than the IC and CR5 populations in Grande Naine and Pisang mas, root necrosis for CR1 was not different from IC and CR5. Severe root necrosis was observed in Pisang Jari Buaya in spite of low Pf for most populations. Similar values of root necrosis were observed for IC and CR5, even though only IC had a high reproductive factor in this resistant host. Root necrosis in the non-inoculated control varied among the banana genotypes. The least necrosis was observed in Pisang Jari Buaya, followed by Pisang mas and Grande Naine.

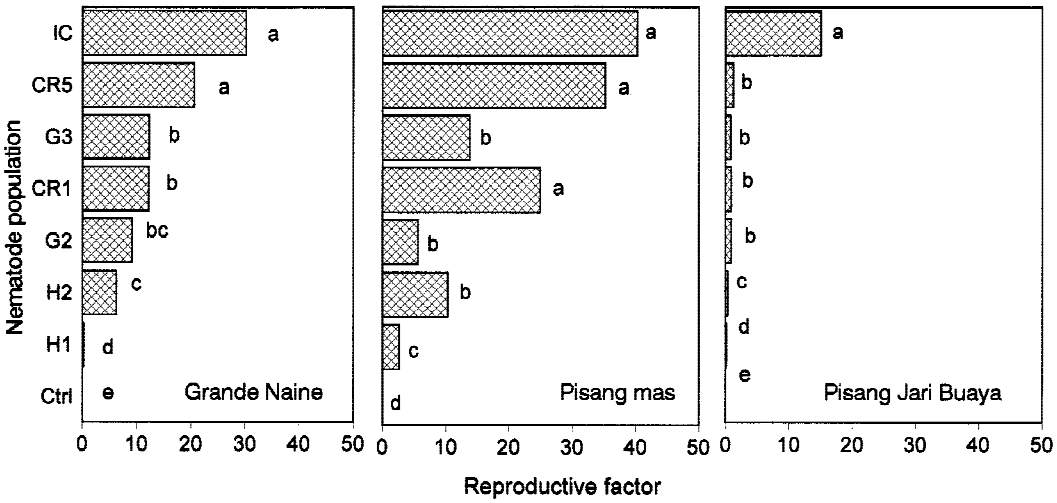

FIG. 4. Reproductive factors of *Radopholus similis* populations extracted from roots of three banana genotypes 8 weeks after inoculation. Reproductive factor = final population/initial population. Bars within a cultivar followed by a common letter are not different according to the Waller-Duncan *k*-ratio ($k = 100$) *t*-test. Ctrl: uninoculated control.

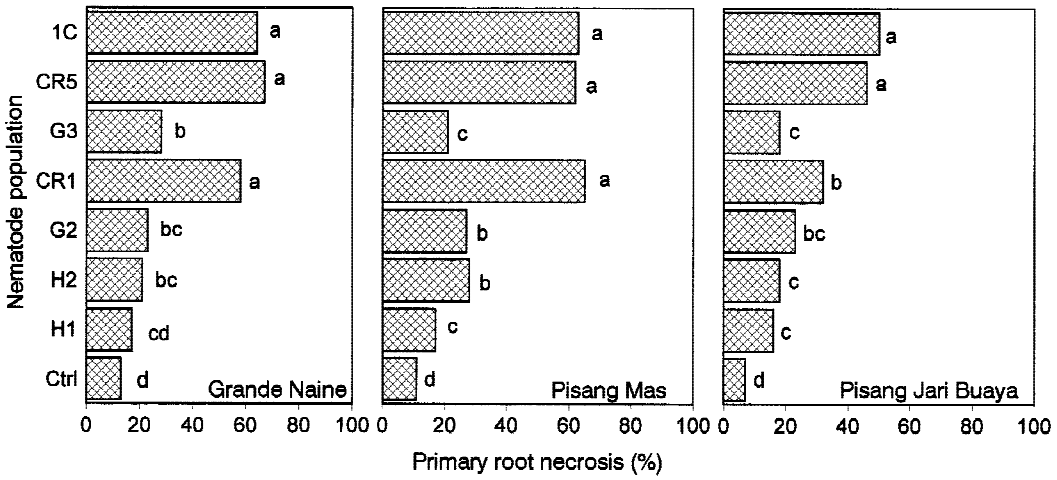

FIG. 5. Primary root necrosis of three banana genotypes 8 weeks after inoculation with different burrowing nematode populations within a cultivar. Bars within a cultivar followed by a common letter are not different according to the Waller-Duncan *k*-ratio ($k = 100$) *t*-test. Ctrl: uninoculated control.

DISCUSSION

Aggressiveness among burrowing nematode populations from Latin America and the Caribbean varied significantly. The reproductive fitness (Rf and nematodes per gram of root) and damage potential of the populations tested in this study were in agreement with damage reported in the field. A population from Guapiles, Costa Rica (CR1), had one of the highest Rfs and root necrosis on susceptible Grande Naine, which suggests that CR1 is highly aggressive. These results are consistent with previous reports by Pinochet (1979, 1988b, 1996) and Tarté et al. (1981).

Populations from Honduras (H1 and H2) and Belize (B) had lower Rf's on susceptible banana than CR1, which agrees with Pinochet (1988b). The population H1 showed a higher Rf and root necrosis than expected from reported damage in field studies (Pinochet, 1988b). This suggests that other factors might play an important role in limiting aggressiveness of the nematode under field conditions.

Little or no detailed information is available on potential variation in aggressiveness of burrowing nematodes in Guatemala. It is believed that suppressive soils are present in this banana-growing area because of the small losses from uprooting in some farms (M. Guzman, Del Monte-Guatemala, pers. comm.). G3 had a higher reproductive factor than G2 and G1. Population G1 came from an area considered suppressive; however, its Rf was the lowest of all the banana populations we tested. The low Rf observed in G1 may play an important role in the limited damage reported in this area.

Although nematode populations differed in their effects on plant-growth variables, none of these parameters reflected the aggressiveness of the burrowing nematode populations tested under our experimental conditions. Total root necrosis and especially the necrosis of primary roots were good indicators of the reproductive fitness of the nematode populations on susceptible hosts. Because some root necrosis always occurred with our technique, even in the noninoculated controls and with less aggressive populations, primary-root necrosis proved to be a better index of aggressiveness than total root necrosis. The small closed container and the sand medium used gave consistent results but apparently were responsible for the background root necrosis in these tests. Overestimation of the damage potential of a weak or less aggressive population would be less likely when using this variable. The short duration of these experiments probably had an important effect on determining significant differences. Fallas et

al. (1995), Hahn et al. (1996), and Sarah et al. (1993) found that root weight was a good indicator of reproductive fitness. Plant height did not correlate well with nematode reproduction under growth-chamber conditions (Fallas et al., 1995; Hahn et al., 1996), although it did under field conditions (Hahn et al., 1996). Duration of experiments limits the use of plant-growth variables tested herein. Hahn et al. (1996) showed that the relationship between growth suppression and nematode aggressiveness was dependent on the duration of the test. In spite of a close relationship between Rf and damage potential (determined by root necrosis assessments), both variables are required to evaluate aggressiveness of populations. The use of both variables is important because there are some situations where high reproductive fitness may not reflect high damage to the root system in banana (Hahn et al., 1996; Marin, 1997, unpubl.).

Reproductive fitness varied only slightly between the two susceptible hosts, Grande Naine and Pisang mas. There was evidence of specific interactions of the seven nematode populations and the susceptible genotypes tested. All populations except IC reproduced poorly in the resistant host, Pisang Jari Buaya This is the first report of a burrowing-nematode population parasitizing this important source of resistance to *R. similis* and the existence of resistance-breaking (virulence) genes to the Pisang Jari Buaya group. The IC population and the population from Uganda also reproduced well in Yangambi Km 5, another known source of resistance to *R. similis* (Hahn et al., 1996). These results suggest that some African populations may have a more variable pool of genes for parasitism than the populations found in the New World. Although recent research indicates that *R. citrophilus* and *R. similis* should be considered as one species (Kaplan et al., 1996), the former did not reproduce on banana.

Results from our study re-emphasize the need to fully characterize the genetic variation of *Radopholus* spp. worldwide. This information is necessary to strengthen breeding programs and improve the strategies and tactics for integrated nematode control in the different banana-growing areas of the world.

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