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Plant Nutrient Partitioning in Coffee Infected with *Meloidogyne konaensis*

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Abstract: Two experiments were conducted to assess nutrient partitioning in coffee (*Coffea arabica* cv. Typica land race Guatemala) infected with *Meloidogyne konaensis*. Nutrient levels were quantified from soil, roots, and leaves. In the first experiment, 500-cm^3 aliquants of a Kealakekua Andisol were infested with four initial population densities of *M. konaensis* ranging from 0 to 1,500 freshly hatched second-stage juveniles. Coffee plants (~3 months old) were transplanted into the soil and grown for 25 weeks. Plants responded to nematode infection with decreases ($P < 0.05$) in concentrations of Ca, Mg, P, and B and increases ($P < 0.05$) in concentrations of Mn, Cu, Zn, and Ca/B in the roots. Mn and Cu uptake by roots was decreased ($P < 0.05$) by nematode infection even though concentrations of Mn and Cu increased ($P < 0.05$) in the roots. Concentrations of Ca and Mg also decreased ($P < 0.05$) in the leaves, whereas the concentration of Zn increased ($P < 0.05$). In the second experiment, the soil was amended with Zn at 0 or 5 mg/kg soil and infested with *M. konaensis* at 0, 100, 1,000 or 10,000 eggs/1,200 cm^3 soil. Three-month-old coffee seedlings of similar height were weighed and transplanted into pots and then placed in a greenhouse and grown under 50% shade for 23 weeks. Concentrations of P, K, Ca, Mg, Mn, B, and Zn increased in roots of nematode-free plants growing in Zn-amended soil. The beneficial effects due to the Zn amendment were not apparent in nematode-infected plants. Mn, B, and Zn uptake by coffee roots and P and B concentrations in coffee leaves responded similarly. Management of *M. konaensis* is necessary to achieve optimal nutrient management in coffee.

Key words: aluminum, boron, calcium, *Coffea arabica,* coffee, copper, Kona coffee root-knot nematode, macronutrient, magnesium, manganese, *Meloidogyne konaensis,* micronutrient, nematode, phosphorus, plant nutrition, potassium, zinc.

The parasitism of plants by *Meloidogyne* spp. alters nutrient partitioning in the plant (Hussey and Williamson, 1996). The infection of the plant directly impacts nutrient and water relations necessary for plant growth (Hussey and Williamson, 1996), with some of the impact being the removal of nutrients or a reduction of their concentration in plant tissues (Sijmons et al., 1991). The severity of the impact is directly related to the number of nematodes feeding on the roots. Ultimately, the nematode infection disrupts physiological processes throughout the plant and is manifested as stunting, nutritional deficiencies or excesses, wilting, and diminished yields.

Sedentary endoparasites dramatically modify host-root tissue (Hussey and Williamson, 1996), and this modification may account for some of the changes in nutrient uptake and partitioning. The nematode feeding process results in the extraction of syncytial cell contents that surely alters normal partitioning of nutrients. During their development, juveniles of *Heterodera schachtii* withdraw from the syncytium an amount equivalent to four times the total volume of the syncytium (Sijmons et al., 1991). In addition, nematodes feeding on giant cells or syncytia modify the biochemical environment within their host plants (Gommers and Dropkin, 1982), altering the source-sink relationships in the plant in order to meet the parasite's nutritional demands (Dorhout et al., 1993). In split-root plants, N and K ions were mobilized by *Meloidogyne incognita* in above-normal amounts from non-infected fertilized roots to infected, nutrient-deprived roots (Bergeson, 1966). The influx of nutrients from phloem tissue to nematode-induced giant cells in the roots was confirmed using carboxyfluorescein (Dorhout et al., 1993).

The relationship of root-knot nematodes to nutrients in coffee has been demonstrated in Central America and South America. Infection by *M. incognita* reduced concentrations of P, Mg, Fe, Mn, and B and increased those of K and Zn (Goncalves et al., 1995). Effects of *M. exigua* on nutrient uptake and balance were inconsistent. In one case, *M. exigua* infection decreased the uptake of Zn, Cu, B, Fe, and Mn in leaves of Mundo Novo coffee (Bonnetti et al., 1982). Only concentrations of Zn and B were affected in the leaves of Mundo Novo coffee in a 1974 study (Macedo et al., 1974). In another study, N and Ca concentrations were lower in infected coffee than in healthy plants, whereas levels of P, K, and Mg were not affected (Santos et al., 1981). Zinc deficiencies in coffee plants were commonly found on coffee farms throughout Hawaii (Shoji and Ota, 1958); this has proved to be especially so in fields infested with *M. konaensis* (Hue, Schmitt, and Serracin, unpubl. data). In addition, volcanic ash-derived soils (e.g., Andisols) have the ability to bind metallic ions (Bohn et al., 1985) so that Zn is less available for plant uptake. This variation among results may be influenced or explained by inoculum density, plant age, and soil substrate (Fatemy and Evans, 1986; Heffes et al., 1992; Maung and Jenkins, 1959).

The objectives of this study were to determine (i) the effects of *M. konaensis* infection on plant nutrient partitioning in coffee plants grown in the greenhouse and (ii) the effects of soil-applied Zn on coffee nutrition in *M. konaensis*-infected plants.

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Materials and Methods

Two greenhouse experiments were conducted to address the objectives. For both tests, a Kealakekua Andisol was collected from the Kona Experiment Station in Kainaliu, Hawaii. For the first objective, approximately 500 cm^3 of autoclaved soil was placed in each of 24 clay pots (10-cm-diam.) and infested with 0, 75, 300, or 1,500 freshly hatched second-stage juveniles (J2) of an *M. konaensis* population collected from a commercial coffee farm in Kealakekua, Hawaii. Juveniles were extracted from coffee roots using a misting system. Three-month-old seedlings of *Coffea arabica* cv. Typica land race Guatemala were collected at the Kona Experiment Station in Kainaliu, Hawaii, beneath healthy coffee trees free of *M. konaensis*. The seedlings were weighed and sorted into blocks by weight for transplanting into designated pots. Pots were randomized within each of the six replications and placed on a greenhouse bench under 50% shade. The duration of the experiment was 25 weeks. Potted plants were watered daily and fertilized weekly with 3.79 g/L of Peters 20:20:20 (N:P:K) fertilizer (J. R. Peters, Inc., 6656 Grant Way, Allentown, PA 18106).

For the second objective, the soil was air-dried, sieved through a screen with 2-mm openings, divided into two 5-kg portions and placed into plastic bags. $ZnSO_4 \cdot 7H_2O$, dissolved in 1 L water, was applied as a spray to the soil in the plastic bags at 5 mg/kg soil. After Zn application, all soil (amended and non-amended) was incubated at 22 °C for 3 days. Clay pots (15-cm-diam.) were arranged into eight groups (treatments) of six pots (replications)/group. Half of the plots (four groups) were filled with Zn-amended soil (approximately 1,200 cm^3 soil pot) and the other half with non-amended soil. Eggs of *M. konaensis* to be used for inoculum were extracted from gelatinous matrices with NaOCl (Barker, 1985). Eggs were placed in 5 ml water, dispersed on the surface of the soil, covered with a 1-cm layer of soil, and immediately moistened with water. Pots designated for inoculation were infested with 0, 100, 1,000 or 10,000 eggs of *M. konaensis*/1,200 cm^3 soil. Then, 3-month-old seedlings of similar height (~12 cm) were weighed and transplanted into the pots. The potted plants were placed in a greenhouse and grown under 50% shade for 23 weeks. All plants were watered daily and fertilized every 3 weeks with 100 ml KPO_4 (4.34 g/L) and $(NH_2)_2CO$ (3.00 g/L). These nutrient solutions were applied 2 days apart.

Treatments were factorially arranged with two levels of Zn and four levels of nematode Pi and replicated six times. Experimental design was a randomized complete block design.

At termination of each of these two experiments, nematode assay and nutrient analyses were performed. Soil was gently removed by hand from the root systems. The roots were washed with water to remove soil particles. Then, the shoots were separated from the roots and weighed. Roots were cut into 2.5-cm long pieces, mixed, and equally divided into two portions: one for root nutrient analysis and the other for nematode assay. Nematodes were also extracted from 250 cm^3 of sieved soil by a combination of elutriation (Byrd et al., 1976) and centrifugal flotation (Jenkins, 1964). Second-stage juveniles of *M. konaensis* were extracted from root tissue using mist (Seinhorst, 1950).

Nutrient concentrations in soil, roots, and leaves were determined. The fourth pair of leaves from the shoot apex of each plant was collected and analyzed for nutrients (Tamimi et al., 1997). The concentrations of P, Ca, Mg, Mn, Zn, and Al were measured in soil and plant tissues. The plant tissues were also analyzed for Cu and B.

In preparation for nutrient analysis, the plant tissues were washed, dried, and ground. They were washed with a 2% mild detergent solution (Sonneveld and van Dijik, 1982), dried at 80 °C for 48 hours, and ground into fine particles. From each batch of ground tissue, 0.25 g was ashed in a muffle furnace at 500 °C for 4 hours. The ash was dissolved in 1 M HNO_3 and evaporated under a flame-hood at 200 °C. Samples were diluted 80-fold with 0.1 M HCl for final nutrient measurements (Hue et al., 2000).

Soil was air-dried at 25 °C for 4 days and sieved through a screen with 16-mm openings in preparation for nutrient analysis. Nutrients were extracted from 2 g of soil with Mehlich 3 solution (Mehlich, 1984) and filtered through 6S filter paper. Samples were diluted 12.5-fold with Mehlich 3 extractant. The nutrient analysis was performed by the Agricultural Diagnostic Service Center at the University of Hawaii at Manoa using an inductively coupled plasma spectrometer.

Nutrient variables were converted to concentrations (% or ppm) and nutrient uptake (uptake = concentration of nutrient/tissue biomass). Plant nutrient concentration and uptake were related to $\log_{10}$-transformed Pi densities of *M. konaensis* using quadratic and linear regression models. Analysis of variance was used to analyze the effects of time, Pi, and plant tissue on nutrient concentration and uptake, and the effects of Zn amendment, Pi, and Zn X Pi interaction on nutrient concentrations, uptake, and translocation. Waller-Duncan K-ratio *t*-tests were additionally used to separate differences among nematode and Zn treatments.

Results

In experiment 1, most of the nutrients assayed in the roots, leaves, or both were affected by *M. konaensis* infection. The concentrations of the macronutrients Ca and Mg decreased ($P < 0.05$) in roots and leaves as a result of nematode infection; P was similarly affected ($P < 0.05$), but only in the roots (Fig. 1A–C). Regression coefficients indicated that *M. konaensis* affected Ca con-

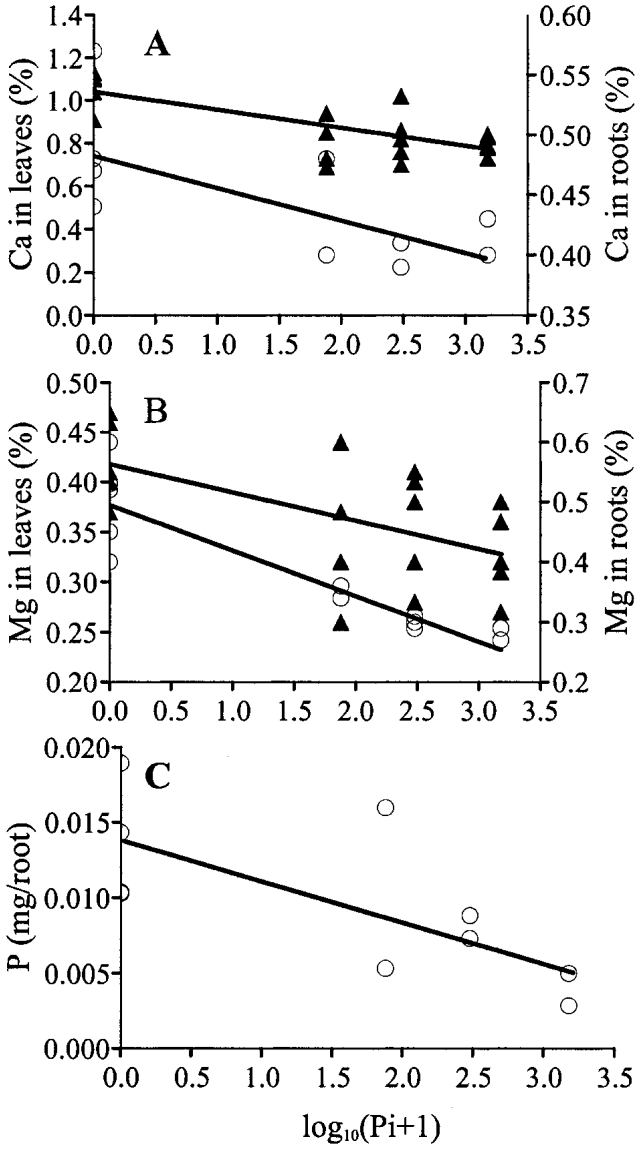

FIG. 1. Relationship between macronutrients in *Coffea arabica* and initial population densities (Pi) of *Meloidogyne konaensis*. A) Ca in leaves = 1.05 – 0.09 [$\log_{10}$(Pi + 1)], R^2 = 0.50; Ca in roots = 0.48 – 0.02 [$\log_{10}$(Pi + 1)], R^2 = 0.43. B) Mg in leaves = 0.42 – 0.03 [$\log_{10}$(Pi + 1)], R^2 = 0.35; Mg in roots = 0.50 – 0.07 [$\log_{10}$(Pi + 1)], R^2 = 0.81. C) P uptake by roots = 0.0139 – 0.0028 [$\log_{10}$(Pi + 1)], R^2 = 0.52. ▲ = leaves. o = roots.

centrations more severely than Mg in leaves, whereas Mg was more severely affected than Ca in roots. Regression coefficients for leaves and roots were –0.09 ($P <$ 0.01) and –0.02 ($P = 0.02$) for Ca and –0.03 ($P < 0.01$) and –0.07 ($P < 0.01$) for Mg (Fig. 1), respectively. K concentrations in roots and leaves were not related to nematode infection.

Uptake of nutrients was affected by nematode infection. Ca and Mg uptake by roots decreased as a consequence of infection by *M. konaensis* (data not shown). P uptake by the roots was lower in nematode-infected treatments than in control treatments (Fig. 1C). At Pi = 1,500, uptake decreased by 71% in comparison to P uptake measured in the controls ($P = 0.01$) (Fig. 1).

Nematode-mediated alterations of micronutrients were most evident in the roots. The concentrations of Mn and Cu increased linearly in relation to nematode Pi (Fig. 2). Mn and Cu were present at 85% and 38% greater concentrations, respectively, at the highest Pi (1,500) ($P = 0.01$) than in the controls (Fig. 2A-B). Mn and Cu uptake by roots was inversely related to their concentrations in the roots. For example, at Pi = 1,500, Mn uptake by roots was 44% less than levels measured in the controls. B uptake by roots and B concentration in the roots decreased ($P < 0.05$) with increasing Pi, the decrease being 43% of the control at the highest Pi (Fig. 2C). Concentrations and uptake of Al were not different among nematode treatments.

Zn concentrations differed more in leaves than in

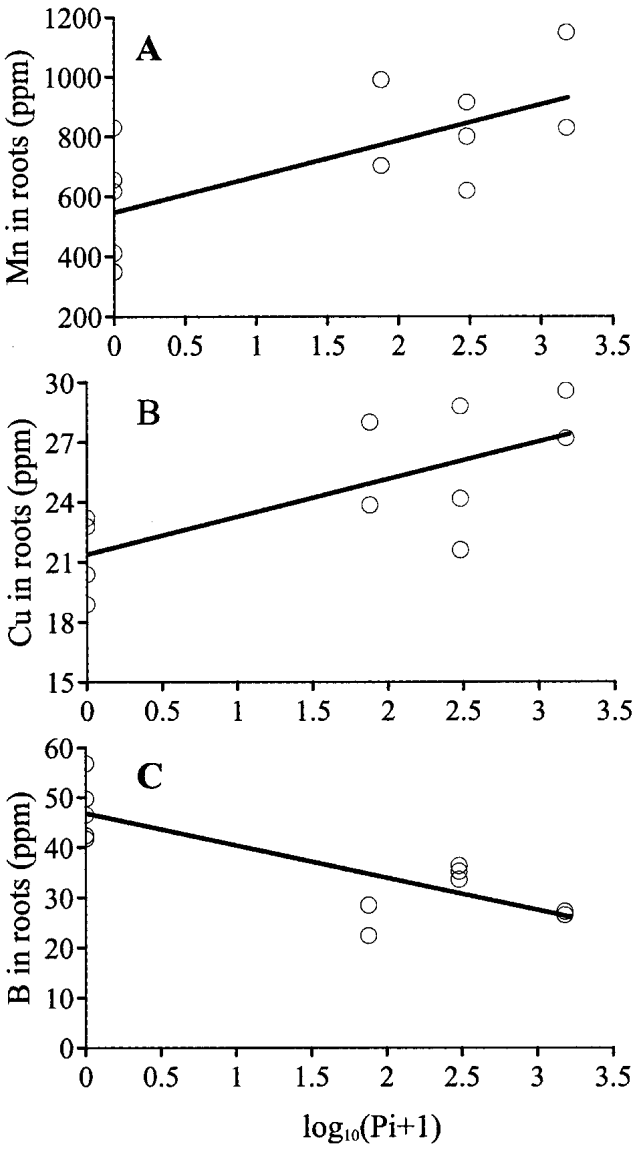

FIG. 2. Relationship between micronutrient concentrations in the roots of *Coffea arabica* and initial population densities (Pi) of *Meloidogyne konaensis*. A) Mn = 537 + 128 [$\log_{10}$(Pi + 1)], R^2 = 0.50. B) Cu = 21.28 + 1.97 [$\log_{10}$(Pi + 1)], R^2 = 0.53. C) B = 46.51 + 6.34 [$\log_{10}$(Pi + 1)], R^2 = 0.67.

roots between nematode treatments. The average concentrations of Zn increased in roots of plants inoculated with 75, 300, and 1,500 *M. konaensis* by about 39% in comparison to Zn in controls ($P = 0.10$) (34 ppm vs. 47 ppm). Zn concentrations were 71% greater ($P < 0.05$) in leaves of infected plants than in uninfected plants (8 ppm vs. 13 ppm).

Meloidogyne konaensis affected the nutrient ratio between Ca and B in roots but not in leaves. The Ca/B ratio in plants infected with nematodes (average of all initial population densities) was 45% greater than in the controls ($P < 0.01$). The Ca/B ratio was 102 in the control plants and 148 in the inoculated plants.

Plant growth was suppressed at all Pi (Fig. 3). Nematode infections severely inhibited coffee growth even at the lowest Pi (75). At this low Pi level, plant growth was suppressed by 58%. At the highest Pi (1,500), little plant growth occurred, resulting in an increase of plant biomass of only 11%. The regression coefficient for nematode Pi vs. change in plant biomass was −3.35 ($P < 0.01$) (Fig. 3).

Infected coffee plants with the greatest change in plant biomass supported the highest levels of MK reproduction. The reproductive factor (R_f = Pf/Pi) was inversely related to Pi ($P = 0.01$). At the termination of the experiment, R_f was 1.32 at Pi = 75 (lowest Pi), 0.44 at Pi = 300, and 0.03 at Pi = 1,500 (highest Pi).

In experiment 2, treatment of the control plants with Zn resulted in a significant ($P < 0.01$) increase in concentration of nutrients in the roots (Fig. 4). This increased nutrient response due to Zn amendment was lost with infection by *M. konaensis*. The nutrient concentrations in infected plants treated with Zn were similar to the concentrations measured in plants without Zn amendment. Nematode infection decreased the concentration of Cu in the roots independent of Zn amendment ($P = 0.02$) (Fig. 4).

Meloidogyne konaensis inoculation and Zn amendment affected uptake of several nutrients (Tables 1, 2). With Zn amendment, any level of nematode infection decreased the uptake of nutrients by the roots (Table 1). Root uptake of P, Mn, and Cu were similarly affected in treatments without Zn amendment. Without Zn amendment, uptake of Ca, Mg, and K decreased at inoculation treatments of 1,000 and 10,000 eggs/pot but not with 100 eggs. Uptake of Zn, B, and Al was not altered in nematode-infected plants. The only nutrient with increased root uptake ($P < 0.05$) in response to Zn application was B (Table 1). In the leaves, both treatments (Zn and *M. konaensis*) altered uptake of P by the leaves (Table 2). P uptake was decreased by all levels of nematode infection if Zn was not applied. With Zn treatment, uptake was reduced only at the 10,000-egg treatment (Table 2). Cu and Zn uptake were reduced by inoculation with 1,000 and 10,000 eggs. Mn uptake decreased with Zn amendment, whereas Cu, Zn, and B uptake by leaves increased with Zn amendment.

In this second experiment, Zn amendment affected neither the reproduction factor of *M. konaensis* nor plant growth at the range of nematode levels (Pi) tested (Fig. 5). R_f was inversely related to the initial population densities in the soil. At the highest Pi, R_f decreased by 64% with respect to the reproduction at the lowest Pi. Nematode Pi was inversely related to plant and root biomass. At the highest Pi, nematodes suppressed plant and root biomass by 50% and 38%, respectively, as compared to the biomass values measured in controls (Fig. 5).

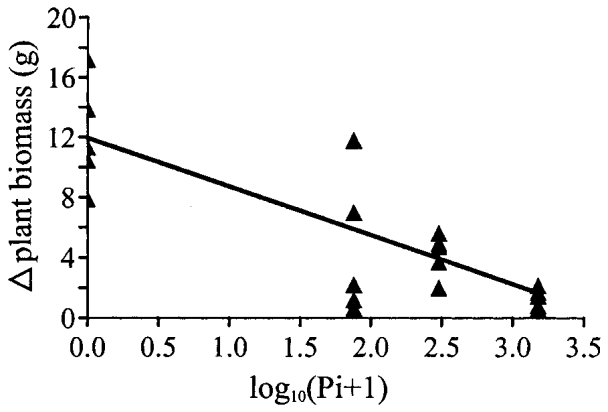

FIG. 3. Change in plant biomass (plant weight at harvest - seedling weight at initiation of the experiment) of *Coffea arabica* in relation to initial numbers of *Meloidogyne konaensis*. △ plant biomass = 11.87 − 3.35[$\log_{10}$(Pi + 1)], $R^2 = 0.67$.

DISCUSSION

Nutrient acquisition may continue within plant tissues even though plant weight does not increase (Yost et al., 2000). The concentration of Mn and Cu in coffee roots increased even though uptake by the roots decreased with increasing nematode inoculum. These results indicate that concentrations of nutrients were affected in plants whose growth was suppressed by nematode infection. For example, the concentration of Mn and Cu was lower in the control plants because leaf biomass was greater in these plants and there were more roots available for uptake than in infected plants. Therefore, Mn and Cu uptake per unit root in healthy plants decreased with respect to the total weight of the entire root system.

Nutrient reductions occurred in coffee leaves presumably because nematode infection damaged the plant's root system, thereby reducing its efficiency for nutrient uptake. When nutrient levels become deficient in plants due to nematode infection, normal physiological processes (i.e., photosynthesis, respiration, and transpiration) are disrupted throughout the whole plant (Melakeberhan and Webster, 1993). In these coffee experiments, the concentration of Ca was low in leaves of plants infected with *M. konaensis*. Ca deficiency in plants contributes to poor root growth (Glass, 1989;

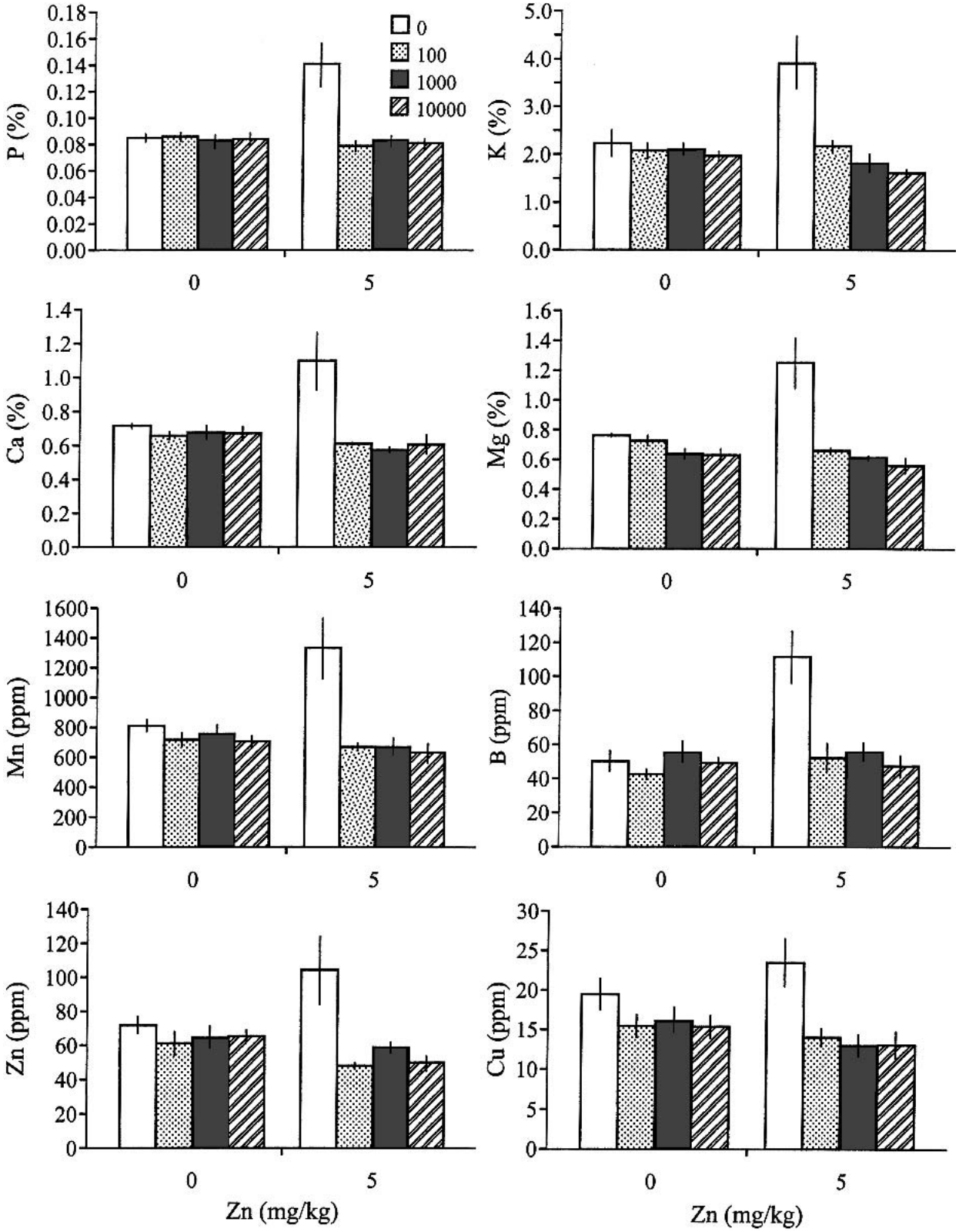

FIG. 4. Concentration of nutrients in the roots of *Coffea arabica* in response to inoculation with *Meloidogyne konaensis* and treated with Zn. Error bars = standard error.

Ramalho et al., 1995). Problems in root growth occur because Ca^{2+} ions function in the stabilization of the cell wall and plasma membrane. Ca^{2+} is an enzyme activator to α-amylase and membrane ATPases (Glass, 1989). Furthermore, Ca deficiency in coffee is associated with decreases in total chlorophyll and the chlorophyll a/b ratio (Ramalho et al., 1995). These factors, along with the root-knot nematode's ability to mobilize

TABLE 1. Nutrient uptake by roots of *Coffea arabica* cv. Typical land race Guatemala at 23 weeks as influenced by Zn treatment (0 or 5 mg/kg soil) and inoculation with *Meloidogyne konaensis*.

		Macronutrients (mg/root)				Micronutrients (µg/root)				
Eggs/pot	Zn	P	Ca	Mg	K	Mn	Cu	Zn	B*	Al
0	0	0.93a	7.98a	8.40a	24.4a	831a	20.0a	73.6	51.3	3,653
100	0	0.92b	6.96a	7.60a	23.1a	735b	15.8b	62.6	43.5	3,141
1,000	0	0.68b	5.41b	5.08b	17.1b	775b	16.5b	65.8	56.4	2,648
10,000	0	0.63b	4.95b	4.65b	14.5b	724b	15.8b	66.9	50.3	2,910
0	5	1.26x	9.28x	11.00x	35.6x	1365x	24.0x	107x	114x	3,981x
100	5	0.74y	5.89y	6.40y	20.6y	687y	14.4y	49y	53y	2,323y
1,000	5	0.57y	3.91y	4.21y	12.6y	685y	13.3y	60y	57y	2,233y
10,000	5	0.53y	4.04y	3.69y	10.7y	647y	13.4y	51y	49y	2,352y

Letters (a,b) represent differences among nematode inoculation treatment means (within columns) for the 0 mg Zn/kg soil treatment according to the Waller-Duncan K-ratio t-test. Letters (x, y) represent differences among nematode inoculation treatment means (within columns) for the 5 mg Zn/kg soil treatment according to the Waller-Duncan K-ratio t-test.

* Means between Zn treatment were different ($P < 0.05$) (within columns) according to general linear model analysis.

nutrients to infection sites (Bergeson, 1966), may foster disruption of optimal nutrient partitioning in coffee.

Meloidogyne konaensis may disrupt Ca translocation from the roots to the shoot. Blevins et al. (1995) described the distribution of Ca in soybean plants infected with *H. glycines*. Calcium translocation decreased in the diseased plants whereas Ca uptake by the roots increased. Females contained high amounts of Ca (4.68 mg/g) and may be acting as Ca^{2+} sinks (Blevins et al., 1995). If *M. konaensis* behaves similarly to *H. glycines,* then it is probably causing sequestration of Ca^{2+} ions from the plant to the giant cells.

Typical chlorosis symptoms on nematode-infected plants are generally associated with decreased chlorophyll content and photosynthetic rates (Melakeberhan et al., 1985; Meon et al., 1978). The Mg^{2+} ion is a major component of the chlorophyll molecule and is essential for the enzyme activity of phosphotransferases (Glass, 1989). Therefore, nematode-infected coffee plants with low Mg levels also may have low chlorophyll contents and low rates of photosynthesis. Coffee plants (cv. Mundo Novo) infected with *M. incognita* race 1 had 37% less Mg and 20% less chlorophyll content in the leaves with respect to concentrations measured in controls (Goncalves et al., 1995). In our work, Mg in coffee leaves and roots was lower in *M. konaensis*-infected plants than in the control coffee plants.

Contradictory results in the literature have been shown for root-knot nematode effects on Ca and Mg partitioning in coffee leaves. In *M. incognita* race 1 infected Mundo Novo coffee, the concentration of Ca was greater, and the concentration of Mg was lower than in noninfected plants (Goncalves et al., 1995). *Meloidogyne exigua* had no effect on the Ca and Mg concentrations in Mundo Novo even at 14 months post-inoculation (Macedo et al., 1974). In another study with Mundo Novo and *M. exigua,* Ca concentration decreased whereas Mg concentration remained unchanged (Santos et al., 1981). In the present experiment with *M. konaensis,* the concentration of both Ca and Mg generally decreased in response to infection.

Zinc deficiencies in coffee plants are commonly found in coffee farms throughout Hawaii (Shoji and Ota, 1958). In the coffee-growing region in Kona, Hawaii, Zn deficiency is associated with coffee decline caused by *M. konaensis*. Soils derived from volcanic ash (e.g., Andisol) have the ability to bind metallic ions (Bohn et al., 1985) so that Zn is less available for plant

TABLE 2. Nutrient uptake by leaves of *Coffea arabica* cv. Typica land race Guatemala at 23 weeks after treatment with Zn (0 or 5 mg/kg soil) and inoculation with *Meloidogyne konaensis*.

		Macronutrients (mg/leaf)				Micronutrients (µg/leaf)				
Eggs/pot	Zn	P*	Ca	Mg	K	Mn*	Cu*	Zn*	B*	Al
0	0	0.24a	4.28	1.30	9.35	279	1.64b	2.0b	13.8	28.3
100	0	0.20b	4.38	1.25	8.25	289	1.27b	1.6b	13.1	28.6
1,000	0	0.20b	4.42	1.27	9.75	283	1.79a	2.6a	15.1	28.5
10,000	0	0.18b	4.63	1.23	9.16	273	1.88a	2.9a	12.7	29.7
0	5	0.30x	4.71	1.40	8.85	248	2.04	3.9	41.1x	28.8
100	5	0.32x	5.03	1.42	9.17	271	2.44	3.3	18.2y	29.4
1,000	5	0.29x	4.70	1.35	10.80	196	2.93	4.7	15.8y	28.4
10,000	5	0.23y	4.23	1.21	11.03	215	1.85	2.7	14.7y	28.1

Letters (a,b) represent differences among nematode inoculation treatment means (within columns) for the 0 mg Zn/kg soil treatment according to the Waller-Duncan K-ratio t-test. Letters (x, y) represent differences among nematode inoculation treatment means (within columns) for the 5 mg Zn/kg soil treatment according to the Waller-Duncan K-ratio t-test.

* Means between Zn treatment were different ($P < 0.05$) (within columns) according to general linear model analysis.

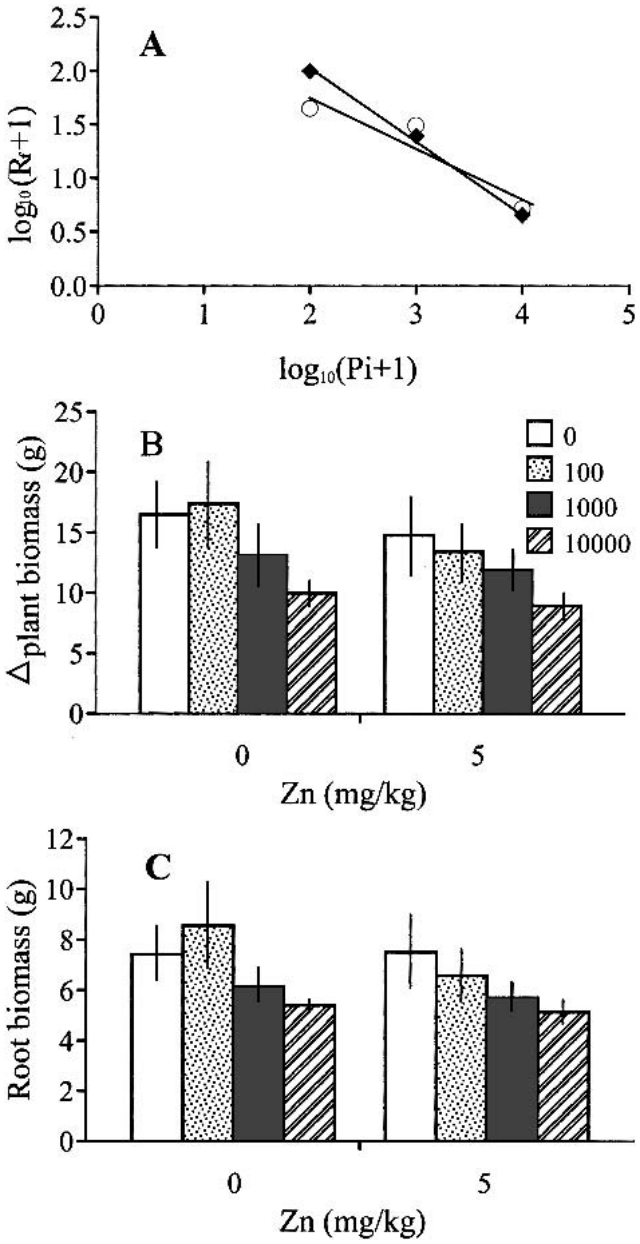

FIG. 5. Reproduction of *Meloidogyne konaensis* and change in coffee biomass (plant weight at harvest—seedling weight at initiation of the experiment) of *Coffea arabica* as affected by initial population density (Pi) of *Meloidogyne konaensis* and Zn amendment. A) Relationship of initial population density to the reproduction factor of the nematode. o = 0 mg Zn/kg soil. ▲ = 5 mg Zn/kg soil. $Log_{10}(R_f+1)_0 = 2.64 - 0.48[\log_{10}(Pi+1)]$, $R^2 = 0.88$; $\log_{10}(R_f+1)_5 = 3.34 - 0.69[\log_{10}(Pi+1)]$, $R^2 = 1.00$. B) Change in total plant fresh weight. △ plant $biomass_0 = 16.62 + 1.81[\log_{10}(Pi+1)] - 0.89[\log_{10}(Pi+1)]^2$, $R^2 = 0.95$; △ plant $biomass_5 = 15.29 - 1.36[\log_{10}(Pi+1)]$, $R^2 = 0.87$. C) Root fresh weight. Root $biomass_0 = 7.50 + 1.11[\log_{10}(Pi+1)] - 0.43[\log_{10}(Pi+1)]^2$, $R^2 = 0.82$; Root $biomass_5 = 7.59 - 0.61[\log_{10}(Pi+1)]$, $R^2 = 0.98$.

uptake. Most likely, though, coffee plants do not translocate enough Zn to leaves to meet the plant's demand (Hue, unpubl. data) because the concentration of Zn is many times greater in roots than in leaves (Hue et al., 2003; Hurchanik et al., 2003). Also, *M. konaensis* and (or) the giant cells may be accumulating Zn ions from roots, as occurred in the cyst bodies of *H. glycines,* which accumulate high amounts of Zn (~72 µg/g) from soybean plants (Blevins et al., 1995).

The addition of Zn to the soil resulted in an increase in the concentration and uptake of Zn and several other nutrients in the roots of coffee. In plants, Zn acts as a cofactor to more than 80 metalloenzymes, such as dehydrogenases, aldolases, phosphostases, and DNA and RNA polymerases (Glass, 1989). Thus, the addition of Zn might have activated various enzymes that function with other inorganic nutrients. P increases in coffee leaves after the addition of Zn when extractable P in soil is at least 60 mg/kg (Raju and Desphande, 1986). Likewise, P in coffee leaves and roots increased in response to the application of Zn to the soil that had more than 70 mg P/kg soil.

The benefits of Zn amendment were no longer apparent when nematodes were added to the system. Even at the lowest nematode inoculum level, concentrations of several nutrients decreased in coffee roots. Nematodes impair the assimilatory function of root systems for nutrient uptake (Hussey and Williamson, 1996). Therefore, the plant's roots cannot function properly in their role to supply nutrients essential for the normal functioning of plants. Due to the root damage by nematodes, increasing fertilizers or organic matter inputs will not compensate for the plant's intolerance to nematode infection (Cadet, 1998).

Some plants have the ability to immobilize trace elements such as Zn and sequester them in certain plant tissues (Hagemeyer and Breckle, 1996). In the field, coffee grown in soil with extractable Zn concentrations as great as 50 mg/kg is Zn deficient in leaves even though the concentrations of Zn are extremely high in roots (Hurchanik et al., 2003). This suggests that coffee may accumulate Zn in roots but cannot translocate it efficiently to leaves. It is further speculated that Zn may be aggregating on the surface of the root, rather than being stored in the vacuoles of the root cells (Hue, unpubl.).

The addition of Zn to the soil affected plant nutrition. The effects of Zn on the nutrient levels within the plant depended on nematode Pi and the amount of Zn available in the soil. Plants that were not infected with *M. konaensis* benefited most from the application of Zn. The beneficial effects of Zn amendment were lost once plants were infected with the nematode.

Balancing nutrients in plants is difficult to accomplish when plant-parasitic nematodes cause nutrient imbalances within the plant. Critical nutrient relationships exist in coffee according to the following nutrient relationships: Ca/B, K/B (Sarruge and Malavolta, 1970), K+Ca+Mg and N/P (Wrigley, 1988). Both Ca and B decreased in the roots due to infection by *M. konaensis,* but the response of the Ca/B ratio indicated that the proportion of Ca was higher in the roots in comparison to the proportion of B. In addition to

nematode effects, imbalanced nutrient supply in the soil also contributes to nutritional imbalances within the plant. Mundo Novo coffee responds best when Ca and B are supplied equally (Sarruge and Malavolta, 1970). If Ca is removed from the substrate, then B supply becomes inadequate. B deficiencies also occur when Ca levels are high in the soil (Willson, 1985). In turn, low levels of B in the soil can restrict Ca uptake (Willson, 1985). Considering all of these factors affecting nutrient balance, it is likely that coffee growth problems are closely related to imbalances due to *M. konaensis* infections.

Soil fertility problems can be corrected by optimizing fertilization regimes (Ramirez, 1998), but this strategy is problematic when the soil is infested with *M. konaensis.* If increasing fertilizer rate stimulates root growth, then the rate of nematode development increases (Oteifa, 1953) followed by an increase of the nematode population density (Schmitt and Riggs, 1989). When making fertilizer recommendations for nematode-infested farms, management should first focus on decreasing the nematode population densities before applying fertilizers for optimal plant growth (Cadet, 1998; Hauser, 2000). After low populations are established, replacing susceptible coffee trees with coffee scions grafted onto resistant rootstocks (Schmitt et al., 2001) should enable growers in Kona, Hawaii, to achieve optimal yields on nematode-infested farms.

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