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Biomass Partitioning in Tomato Plants Infected with *Meloidogyne incognita*[1]

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Abstract: Tomato plants were inoculated with *Meloidogyne incognita* at initial populations (Pi) of 0, 1, 10, 50, 100, and 200 (×1,000) eggs per plant and maintained in a growth chamber for 40 days. Total fresh biomass (roots + shoots) at harvest was unchanged by nematode inoculation with Pi of 1×10^5 eggs or less. Reductions in fresh shoot weight with increasing Pi coincided with increases in root weight. Total fresh biomass declined with Pi above 1×10^5 eggs, whereas total dry biomass declined at Pi above 1×10^4 eggs. The greatest reduction percentages in fresh shoot biomass induced by root-knot nematodes occurred in the stem tissue, followed by the petiole + rachis; the least weight loss occurred in the leaflets. Although biomass varied among shoot tissues, the relationship between biomass of various shoot tissues and Pi was described by quadratic equations. The linear and quadratic coefficients of the equations (stem, petiole + rachis, or leaflets on Pi) did not differ among tissues when calculations were based on standardized values. *Meloidogyne incognita*-infected plants had thinner leaves (leaf area/leaf weight) than did uninfected plants. Reductions in leaf weight and leaf area with nematode inoculation occurred at nodes 5–15 and 4, 6–14, respectively. Losses in plant height and mass due to nematodes reflected shorter internodes with less plant mass at each node.

Key words: biomass, *Lycopersicon esculentum, Meloidogyne incognita,* metabolic sink, tomato.

Disease caused by *Meloidogyne* spp. is a complex phenomenon. Acting as metabolic sinks, root-knot nematodes redirect nutrient flow within the plant to the root system and elicit profound changes in root morphology (2,7,11). Giant cell formation and hypertrophy and hyperplasia of surrounding cortical root tissues are symptoms of an altered host metabolism. As obligate sedentary endoparasites, root-knot nematodes require relatively healthy plants which produce sufficient phytosynthate to support nematode development and reproduction. Net photosynthesis is reduced in tomato, bean, and grape seedlings following inoculation with *Meloidogyne* spp. (10,14,17). The decreased photosynthesis occurs soon after inoculation and thus may explain the resulting reduction in plant biomass accumulation.

Root-knot nematodes rapidly utilize carbon fixed in the leaf tissue (12,13) and consume a significant portion of the total energy produced by the plant. The large body size, egg laying capacity, and protein content of *Meloidogyne* spp., in addition to modifications in the structure and physiology of the plant root, reduce the energy status of the host (12,13). Less energy is available for maintaining and expanding plant structures such as leaves, petioles, and stem. Translocation and absorption of nutrients may be altered (4,6,15), and altered nutrient allocation impacts shoot and root formation. As the nematode population increased in *M. javanica*-infected tomato, shoot weight was suppressed and followed a quadratic response, whereas root weight increased linearly (18). As a result of differential biomass partitioning induced by the nematode, a higher root-to-shoot ratio occurred.

Changes induced by root-knot nematodes in partitioning of biomass among shoot tissues have not been studied. An understanding of the effects of nematode

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parasitism on the partitioning of mass among plant tissues may provide insight into how plants respond to nematode-induced stress. It is the purpose of this study to determine the effects of *Meloidogyne incognita* on 1) plant biomass over a range of initial nematode population densities likely to result in shoot weight loss, 2) biomass partitioning among shoot tissues, and 3) the interrelationships between mass changes in nematode-altered plant structures.

Materials and Methods

Culture of plants and preparation of inoculum: Tomato seeds (*Lycopersicon esculentum* Mill. cv. Rutgers) were germinated in vermiculite, and 10-cm-tall seedlings were transplanted into 15-cm-d plastic pots containing 1 liter of a heat pasteurized Varina sandy loam soil (75% sand, 17% silt, 8% clay; pH 6.5, 0.8% organic mater) : sand : Peat-Lite (Conrad Farard, Springfield, MA) (2:2:1 v:v:v) mixture. The plants were maintained in the greenhouse until they averaged 15 cm in height; then they were placed in a growth chamber maintained at 25 ± 1 C with 12-hour days of cool white light at 350 $\mu mol^{-2} \cdot s^{-1}$ between 400 and 700 nm. The plants used in our study were similar in size to tomato plants normally used in field plantings. The *M. incognita* race 3 population was isolated from field plots at the Pee Dee Research and Education Center at Florence, South Carolina, and cultured on Rutgers tomato seedlings. Nematode eggs from 50-day-old tomato roots were extracted in 0.05% sodium hypochlorite, washed in tap water, and used as the inoculum (8). All plants were watered with Hoagland's solution every 7 days (5).

Nematode population density and plant growth: Tomato plants were maintained in the controlled environment chamber for 48 hours and then inoculated with suspensions of approximately 0, 10^3, 10^4, 5×10^4, 10^5, or 2×10^5 eggs. A root suspension filtrate, from nematode-free tomato plants, was added to the control plants and to the inoculated plants with each plant receiving 20 ml suspension. Inoculum was pipetted into two 5-cm-deep holes on opposite sides of each tomato plant, and the holes were covered with soil. Plant growth and nematode development were evaluated after 40 additional days in the growth chamber. Plants were removed from the pots, and roots were washed free of soil. Each plant was divided into stems, leaves (petiole detached at the stem), and roots. Plant parts were weighed, and internode lengths were recorded. Leaf area was determined with a Li-Cor model 3100 area meter (Li-Cor, Lincoln, NE). Each leaf was then separated into the petiole + rachis and leaflets, and tissues were weighed. Root galling was rated on a 0 to 10 scale: 0 = no galls and 10 = 100% of the root tissue galled (1). Roots in 0.05% sodium hypochlorite were blended for 15 seconds at low speed to enhance the recovery of nematode eggs (8). Nematode data were transformed, $\log_{10}(x + 1)$.

A randomized complete block design with five replications was used, and the test was repeated once. Because results were similar for both tests, data were pooled and analyzed using analysis of variance (ANOVA) and regression techniques (16). Mean comparisons were used to determine the effect of initial nematode population levels (Pi) on mass of specific plant tissues. Nonlinear regression (quadratic) was used to compare the responses of different plant tissues to the nematode. Quadratic regressions were used because the linear and quadratic coefficients can easily be compared among equations. Comparisons between exponential regressions are more difficult to interpret. Because low Pi ($<10^3$) were not examined, conclusions about stimulatory or inhibitory effects of low nematode populations cannot be made with these data. Linear and quadratic coefficients were compared among line equations with a *t*-test. All calculations were performed with the Statistical Analysis System (SAS Institute, Cary, NC) general linear models procedure. For some comparisons, data were converted to a standardized scale (3) using equation 1, where $\bar{X}$ = the average of 10

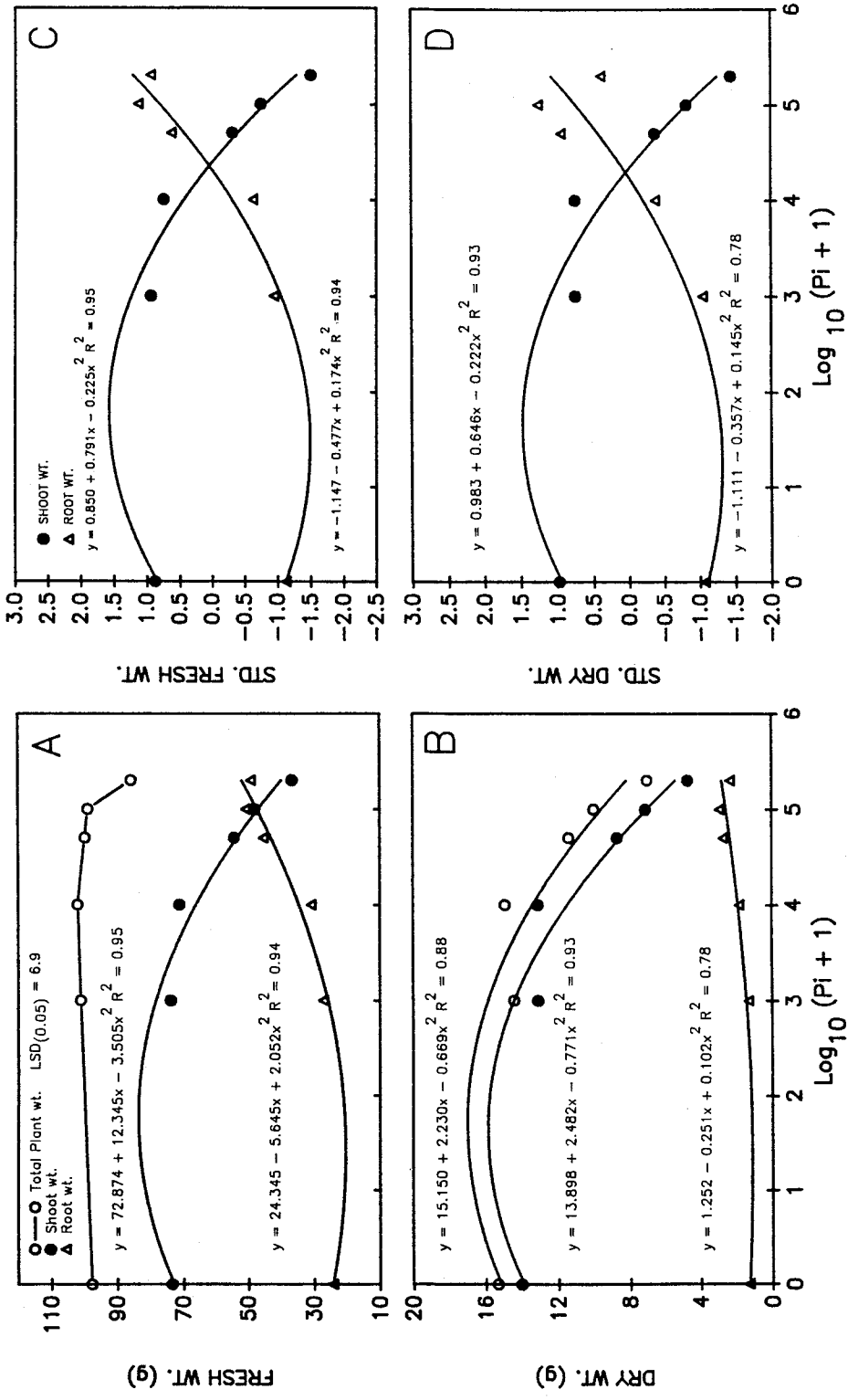

FIG. 1. Effect of initial *Meloidogyne incognita* population density (Pi) on biomass of Rutgers tomato 40 days after inoculation. Values are means of 10 replications. Regressions were based on means. A, B) Root, shoot, and total fresh and dry weights. C, D) Standardized shoot, root, and total fresh and dry weights. Responses were centered and scaled to a mean of 0 and a variance of 1.

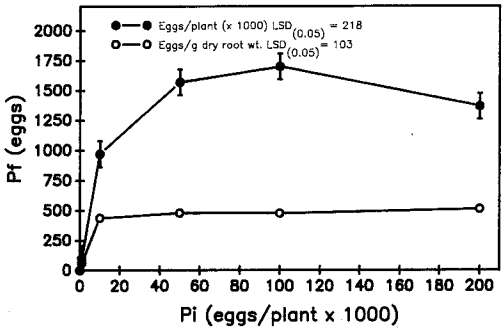

FIG. 2. *Meloidogyne incognita* eggs extracted from tomato roots 40 days after inoculation. Pi = initial population; Pf = final population. Values are the means of 10 replications.

replications of parameter X at inoculum level i, $\bar{\bar{X}}$ = the average of parameter X across all inoculum levels, and SD = the standard deviation of the $\bar{X}$'s from the $\bar{\bar{X}}$ defined as $SD = (\Sigma(\bar{X}_i - \bar{\bar{X}})^2/n - 1)^{1/2}$.

$$\text{Standardized value} = (\bar{X} - \bar{\bar{X}})/SD \quad \text{(Eq. 1)}$$

Equation 1 centers and scales the responses to a mean of 0 and a variance of 1.

RESULTS

The fresh shoot weight of tomato plants inoculated with more than 1×10^4 *M. incognita* eggs was less ($P = 0.05$) than that of uninoculated controls (Fig. 1A). The decline in shoot weight was matched by an increase in fresh root weight (Fig. 1A) at

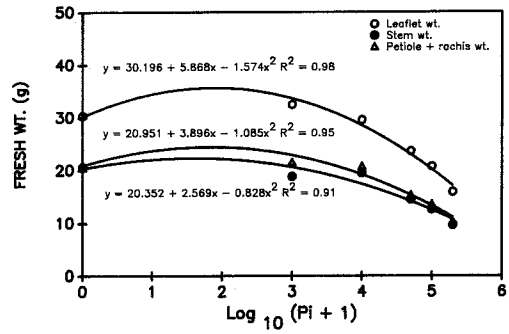

FIG. 3. Effect of initial *Meloidogyne incognita* population density (Pi) on leaflet, petiole + rachis, and stem weights of Rutgers tomato 40 days after inoculation. Values are means of 10 replications. Regressions were based on means.

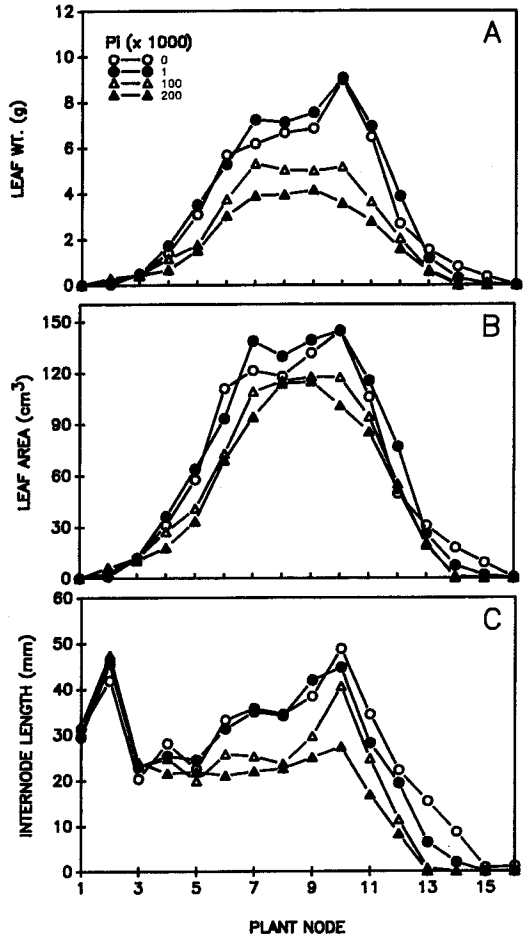

FIG. 4. Leaf weight, leaf area, and internode lengths of Rutgers tomato plants 40 days after inoculation with *Meloidogyne incognita*. Pi = initial nematode population. A) Leaf weight. B) Leaf area recorded at each node. C) Internode lengths (cotyledon to node 1 = plant node 1). Values are the means of 10 replications.

Pi levels between 1×10^4 and 1×10^5 eggs ($P = 0.05$). The decline in shoot mass and the increase in root mass with increasing Pi were described by quadratic equations $P = 0.01$ and $P = 0.04$, respectively. Linear and quadratic coefficients (absolute values) of the regressions, based on standardized data for fresh shoot and root weights, were not different ($P = 0.05$) (Fig. 1C). Total fresh weight biomass declined ($P = 0.05$) when Pi exceeded 1×10^5 eggs/plant (Fig. 1A).

Dry shoot weight and total dry biomass declined at a Pi greater than 1×10^4 eggs;

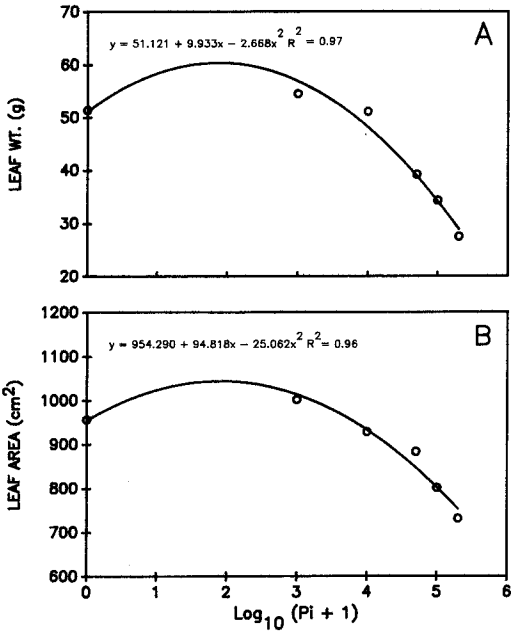

FIG. 5. Effect of *Meloidogyne incognita* population density (Pi) on leaf area and leaf weight of Rutgers tomato 40 days after nematode inoculation. Values are means of 10 replications. Regressions were based on means. A) Leaf weight. B) Leaf area.

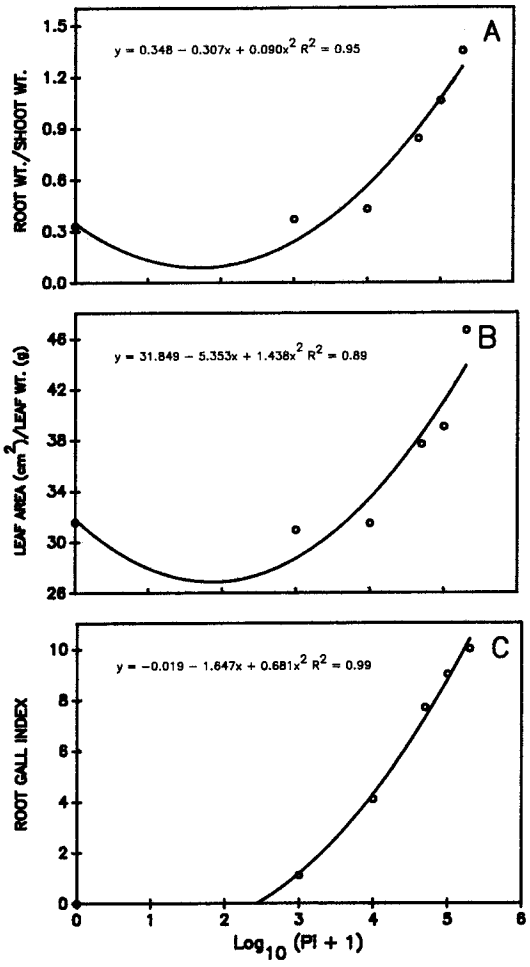

FIG. 6. Root/shoot weight ratio, leaf area/leaf weight ratio, and root galling of Rutgers tomato 40 days after inoculation with *Meloidogyne incognita*. Pi = initial nematode population. Values are means of 10 replications. Regressions were based on means. A) Root/shoot weight. B) Leaf area/leaf weight. C) Root gall index.

the declines in shoot and total weights were described by quadratic equations $r^2 = 0.93$, $P = 0.03$ and $r^2 = 0.88$, $P = 0.06$, respectively (Fig. 1B). Dry root weights of *M. incognita*-infected tomato plants were greater ($P = 0.05$) than those of controls with Pi levels of 1×10^4 eggs or greater. Linear and quadratic coefficients (absolute values) of the regressions for dry shoot and root weights on Pi, based on standardized data, were not different ($P = 0.05$) (Fig. 1D).

The number of eggs at harvest (Pf) increased with Pi up to 1×10^5 and then declined at the highest Pi (Fig. 2). In contrast, the Pf/g dry root weight increased to a maximum level with a Pi of 1×10^4 and then remained constant at higher Pi (Fig. 2).

Stem, petiole + rachis, and leaflet weights of *M. incognita*-infected plants were less than those of control plants at Pi greater than 10^3; the declines in stem, petiole + rachis, and leaflet weights were described by quadratic equations $r^2 = 0.91$, $P = 0.05$; $r^2 = 0.95$, $P = 0.01$; and $r^2 = 0.98$, $P = 0.001$, respectively (Fig. 3).

The reduction in top weight was not uniformly distributed across shoot tissues. The percentage of reduction in shoot tissue weights, when averaged across Pi, was greatest ($P = 0.05$) in the stem tissue (28%), intermediate in the petiole + rachis (24%), and least in the leaflets (20%). The decline in stem weight due to nematode parasitism was 38% greater than the decline in leaflet weight.

Reductions in internodal leaf weight and leaf area with nematode inoculation occurred at nodes 5–15 and 4, 6–14, respec-

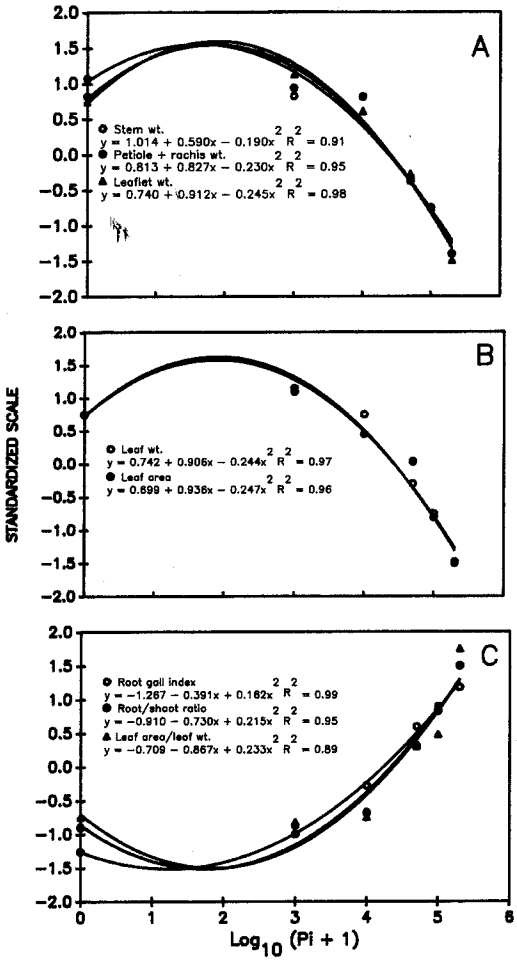

FIG. 7. Standardized growth parameters plotted as a log function of the initial nematode population (Pi), $\log_{10}$ (Pi + 1). Responses were centered and scaled to a mean of 0 and a variance of 1. Regressions were based on means. A) Stem, petiole + rachis, and leaflet weights. B) Leaf weight and leaf area. C) Root gall index, root/shoot ratio, and leaf area/leaf weight ratio.

tively (Fig. 4A, B). Internode length was reduced above node 3 (Fig. 4C). The percentage of change in leaf weight and leaf area from internode to adjacent internode (starting at node 3 to 4) was unaffected by Pi levels ($P = 0.05$). The percentage of change in internode lengths varied ($P = 0.05$) with Pi between internodes 5–6, 6–7, and 12–13.

As the Pi increased, leaf area and leaf weight decreased ($P = 0.05$) and were described by quadratic equations $r^2 = 0.96$, $P = 0.01$ and $r^2 = 0.97$, $P = 0.01$, respectively (Fig. 5). Leaf weight declined at a faster rate than did leaf area.

The root/shoot ratio, leaf area/leaf weight ratio, and root gall index increased with Pi (Fig. 6) and were described by quadratic equations $r^2 = 0.95$, $P = 0.01$; $r^2 = 0.89$, $P = 0.04$; and $r^2 = 0.99$, $P = 0.001$, respectively.

Although the percentage of reduction in mass due to *M. incognita* varied among shoot tissues, the linear and quadratic coefficients of the equations, based on standardized data, were not different ($P = 0.05$) (Fig. 7A). The percentage of reduction in leaf weight due to *M. incognita*, when averaged across Pi, was 28% and was greater ($P = 0.05$) than the percentage of reduction in leaf area (8%). The linear and quadratic coefficients of the equations for leaf weight and leaf area, based on standardized data, were not different (Fig. 7B). The effects of Pi on standardized values for root gall index, root/shoot ratio, and leaf area/leaf weight were described by quadratic equations, and the linear and quadratic coefficients of the line equations were not different ($P = 0.05$) (Fig. 7C).

DISCUSSION

Biomass accumulation of *M. incognita*-infected tomato plants reflects the efficiency of the parasite-altered host to capture light energy and store that energy in the structures of the plant and nematode (10,14). Fresh shoot weights of tomato declined with increasing numbers of *M. incognita* as expected, but a similar increase in fresh root weight balanced the loss with a Pi as high as 1×10^5 eggs. The relatively high ratio of fresh root to shoot weight vs. the ratio of dry weights suggests that fresh roots contain more water than do fresh shoots. Dry weights provide a more realistic measure of the effects of the nematode on the partitioning of mass; in the field, reductions in shoot growth greatly exceed increases in root growth.

Changes in dry root mass were minor compared to the dramatic reductions in shoot weight. However, a strong relationship was observed between the decline in

shoot weight and the corresponding increase in root weight when data were standardized. The use of standardized values allows the changes in plant mass due to root-knot nematodes to be viewed from a different perspective. When responses are centered and scaled to a mean of zero with a variance of 1, comparisons can be made between the shapes of the response curves independent of the magnitude of the response. Many tissues had similar response curves when data were standardized which may have implications for the host-parasite relationship.

Plant shoot tissues were altered disproportionately by *M. incognita*; stems were more affected than petiole + rachis, and leaflets were least affected. The disproportionate changes in plant mass of specific shoot tissues may reflect an adaptive mechanism to plant stress and may be associated with changes in the growth regulator balance of plants infected by root-knot nematodes. The lowest reduction percentages in fresh or dry weights over an uninoculated control occurred in the leaf tissue. In addition, leaf area declined very little. The increase in the leaf area/leaf weight ratio with increasing Pi maximizes light interception with less leaf mass. Increases in leaf area/dry weight ratio (thinner leaves) also can be seen in plants that are grown under shade (9).

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