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Resistance

Quantitative Comparison of the Resistance to Phytophthora Root Rot in Three Avocado Rootstocks

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ABSTRACT

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The resistance of three avocado (*Persea americana* var. *drymifolia*) rootstocks to Phytophthora root rot was compared quantitatively in greenhouse experiments. Susceptible seedlings of rootstocks Topa Topa and resistant cuttings of rootstocks Duke 7 and G6 were planted in avocado field soil naturally infested with *Phytophthora cinnamomi* at 0.3–3.1 propagules per gram (ppg) of dry soil. Soil populations of *P. cinnamomi*, percent of roots infected per plant, and shoot and root weights were determined after 8, 15, and 20 wk. At 20 wk, root infection was 55, 27, and 11% in Topa Topa, Duke 7, and G6, respectively. Soil populations after 20 wk were 55, 42, and 14 ppg for Topa Topa, Duke 7, and G6, respectively. Compared to uninfected controls, significant reductions in root weights of infected plants occurred with each rootstock, but the percent reduction was greater with Topa Topa than with Duke 7 or G6. Generally, more propagules were recovered on dilution plates from detached roots infected in culture with zoospores than from attached roots infected in the greenhouse while growing in infested soil. In the absence of *P. cinnamomi*, Duke 7 and G6 had a significantly greater capacity for root regeneration than the susceptible rootstocks Walter Hole and Topa Topa.

Additional key words: root growth potential.

Avocado root rot, caused by *Phytophthora cinnamomi* Rands, is a soilborne disease that seriously affects production of avocado (*Persea americana* Mill.) (15,17). An important approach to control of root rot has been the development of rootstocks with field resistance to *P. cinnamomi* (15). More than 3,000 selections of different *Persea* spp. have been screened for root rot resistance with qualitative methods that include hydroponic tank tests, greenhouse pot tests with infested soil, and long-term field plots in infested sites (16,17). As a result of this screening program, two Mexican avocado selections with some field resistance to avocado root rot, Duke 7 and G6, are available commercially as rooted cuttings. The resistance of Duke 7 and G6 to *P. cinnamomi* has been described by Zentmyer as "moderate horizontal resistance or tolerance" (15). There are, however, no quantitative data on the biological basis of this resistance or on the comparative levels of resistance in these rootstocks.

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Component analysis of the disease cycle has been used to evaluate general resistance in several Phytophthora-host systems (14), but this quantitative approach to evaluating resistance has not been attempted in the interaction of *P. cinnamomi* and avocado.

The purpose of the work reported here was to develop methods of quantitatively comparing the levels of resistance in various avocado selections by analyzing components of the disease cycle.

MATERIALS AND METHODS

Sources of plants, soil, and inoculum. Four to 6-mo-old, root-rot-resistant cultivars Duke 7 and G6, and susceptible cultivars Topa Topa and Walter Hole of avocado [*Persea americana* Mill. var. *drymifolia* (Schlect. and Chamb.) Blake] were evaluated in various experiments. Seedlings of Topa Topa were raised in greenhouses at the University of California, Riverside. Rooted cuttings of Duke 7 and G6, and seedlings of Walter Hole were obtained from either Brokaw Nursery, Saticoy, CA or C and M Nursery, Nipomo, CA. All material was initially propagated in 7× 27-cm plastic sleeves in a greenhouse potting mix of peat and Perlite® (60:40, w/w). Experiments were conducted with a sandy loam avocado field soil (Fallbrook series) collected in San Diego County 2–4 days prior to use. Soil infested with *P. cinnamomi* came

from beneath 12-yr-old avocado trees infected with root rot, and uninfested soil was collected from an adjacent area. Soil moisture of freshly collected soils ranged from 10–15%. All in vitro experiments were performed with an isolate of *P. cinnamomi* (Pc 402) from the infested site.

Prior to use, soils were assayed qualitatively for the presence of *P. cinnamomi* by using seedling traps of *Persea indica* (L.) Spreng. (17). Quantitative assays of the fungal soil population were conducted with a modification of the soil-dilution plating technique of Kannwischer and Mitchell (8). A 50-g (wet weight) soil sample was mixed thoroughly with 100 ml of 0.25% water agar. The dry weight of a 1-ml sample from each soil mixture was determined. A 1-ml sample of the soil suspension was spread over each of 10 petri plates that contained 12–15 ml of an antibiotic medium, PARPH, which is selective for *Phytophthora* spp. This medium was modified from a previous description (8) by the substitution of 125 μg/ml ampicillin trihydrate (85%; Bristol Laboratories, Syracuse, NY) for 250 μg/ml sodium ampicillin, and the addition of 50 μg/ml hymexazol (Sankyo Co., Shigaken, Japan). After 3 days of incubation at 23 C in the dark, plates were rinsed free of soil and colonies were counted. Population was expressed as propagules per gram (ppg) of dry soil by dividing the average number of colonies per plate by the weight of the dried 1-ml sample of the soil-water-agar suspension.

Greenhouse experiments in infested soil. Duke 7, G6, and Topa Topa were compared in greenhouse experiments with soil infested with *P. cinnamomi*. After removal of plastic sleeves, rooted cuttings of Duke 7 and G6 were excised from their nurse seeds and the roots of Topa Topa seedlings were trimmed from the bottom so that root balls of all selections were of approximately equal dimensions (7 × 17 cm). Root balls were transferred intact to cylindrical pots (11 × 18 cm) and surrounded by approximately 900 cm^3 of infested or uninfested soil. Plants were grown in the greenhouse for up to 20 wk. Soil moisture was maintained at field capacity (~20%) by daily watering. The experiment was done three times with five or six replicates in each treatment.

Soil populations of *P. cinnamomi*, percent of infected roots on each plant, root weights, and shoot weights were recorded 8, 15, and 20 wk after planting. To determine populations of *P. cinnamomi*, four soil cores were removed from each pot with a 2 × 11-cm cork borer. The samples were bulked and assayed quantitatively according to the dilution-plate method described above. Plants were rinsed free of soil, and root and shoot weights were recorded. To estimate root infection, forty 1-cm root segments were selected randomly from each plant, surface disinfested for several seconds in 70% ethyl alcohol (EtOH), blotted dry, and plated on PARPH. Recovery of *P. cinnamomi* was recorded after 2 and 3 days of incubation at 23 C in the dark. Root infection was expressed as the percentage of root segments infected as measured by recovery of the fungus from the root pieces. The root weights of infected plants compared to uninfected controls were expressed as a percentage:

$$[(\text{Uninfected root wt}) - (\text{infected root wt})]/[\text{Uninfected root wt}] \times 100 = \text{Percent reduction in root wt.}$$

For each rootstock, the reduction in root growth was related to the amount of infection over time.

Quantitative assessment of fungus in excised roots. A root maceration technique was developed to assay the relative amounts of *P. cinnamomi* within infected roots. Roots infected in the greenhouse and roots infected in culture were compared. For inoculations in culture 1- to 2-cm root tips were excised from rooted cuttings of Duke 7 and G6 or from seedlings of Walter Hole. Two plants of each selection were used in each experiment. Sixty freshly excised root segments of each selection were placed on 0.8% water agar, and the intact root tips were pressed gently into the agar to elevate the cut end from the surface. Zoospores of *P. cinnamomi* were generated with a nonsterile soil extract system (1). One 10-μl drop of a suspension of 10^5 zoospores per milliliter was placed on each root tip. Up to 15 root segments could be inoculated in one 90-mm-diameter petri plate. The viability of zoospores, as measured by germination on water agar, varied from 50 to 80% in different experiments; root infection was 70–90%. After incubation at 24 C for 24 hr in the dark, roots were surface disinfested in 70% EtOH and plated on PARPH. Roots were examined for growth of *P. cinnamomi* after 3 days of incubation at 23 C in the dark. As in other experiments, infected roots were considered to be those from which the fungus grew outward and into the medium.

Two root samples of 20 infected pieces each were retrieved from the agar and the dry weight of one sample was determined. The second sample was surface disinfested in 70% EtOH, blended with 50 ml of distilled water in a Sorvall Omnimixer (two 30 sec bursts at 8,000 rpm) and this macerated suspension was diluted 1:2 or 1:4 with sterile distilled water. One-milliliter samples of each dilution were spread on each of eight replicate plates of PARPH. Colonies were counted after 2 and 3 days. By using the moisture percentages calculated in the dried equivalent sample, the dry weight of root tissue on each dilution plate was estimated. The propagules per gram of dry root tissue was estimated as follows:

$$(\text{Average number of colonies per plate})/(\text{Average dry wt of root tissue per plate}) = \text{Propagules per gram dry root.}$$

Infected roots obtained from plants grown for 20 wk in infested soil were also macerated and dilution-plated as described above. This quantification process was performed twice with infected roots from greenhouse experiments and four times with roots infected in culture.

Comparison of root growth potential. The relative root growth potentials of Duke 7 and G6 were compared to those of Walter Hole and Topa Topa in uninfested avocado field soil in two experiments. Plants were transplanted from plastic sleeves to cylindrical pots (8 × 11 cm) and grown in a greenhouse for 3 wk. Since plants could not survive bare rooting, they were removed from pots keeping the soil intact around the roots and one-half of the root-soil mass was removed longitudinally with pruning shears. The remaining root-soil mass was transplanted into 3.8-L pots and maintained under greenhouse conditions. Control plants were not subjected to root pruning. Each treatment contained seven or eight replicates. After 4 wk, root and shoot dry weights were recorded. Root weights were compared to estimate the root growth potential of each rootstock.

RESULTS

Greenhouse experiments in infested soil. There was a small variation in the level of the initial population of *P. cinnamomi* in infested soil collected for three experiments (0.3, 1.6, and 3.0 ppg dry soil, respectively). This difference in initial inoculum did not affect disease progress over 20 wk as measured by root infection, soil population, and plant weights. So the data from the three experiments were combined for linear regression analysis (Table 1). An analysis of covariance was used to determine significant differences between individual regression lines. Regression lines with unequal slopes were compared with a *t*-test and a *t*-test of adjusted means was used for lines with equal slopes.

Root infection increased with time in both the resistant and susceptible selections (Fig. 1) but was significantly different ($P = 0.01$) among the three rootstocks. After 20 wk, the percentage of roots infected was 55, 27, and 11 for Topa Topa, Duke 7, and G6, respectively.

The soil populations of *P. cinnamomi* increased with time for all three rootstocks, but after 20 wk they were significantly higher for Duke 7 (55 ppg) and Topa Topa (42 ppg), than for G6 (14 ppg) (Fig. 2).

When root and shoot weights of infected and uninfected plants were compared, significant differences were observed among the three rootstocks. Infected and uninfected Topa Topa differed more in their root weights (11.5 and 62.1 g, respectively), than did Duke 7 (25.4 and 29.7 g), or G6 (19.4 and 29.8 g) (Fig. 3). The rates of root growth of infected plants as measured by the slopes of the

regression lines (Fig. 3) were greater for Duke 7 and G6 than for Topa Topa, but these differences were significant ($P = 0.05$) only between G6 and Topa Topa.

When the percent reduction in root weight was related to the amount of infection over time (Table 2), Topa Topa had the highest amount of infection and correspondingly the largest reduction in root weight. Duke 7 had a moderate amount of infection, but there was a relatively low reduction in root weight. G6, with the lowest amount of infection, had an intermediate amount of reduction in root weight, compared to Duke 7 and Topa Topa (Table 2).

TABLE 1. Regression equations of root infection, soil population, root weights, and shoot weights of avocado Topa Topa, Duke 7, and G6 rootstocks relative to time. Data were collected 8, 15, and 20 wk after planting into soil infested with *Phytophthora cinnamomi*

		Regression equation[a]	Correlation coefficient (r)[a]
Root infection vs time			
Topa Topa		$Y = 6.78 + 2.44X$	0.47**
Duke 7		$Y = -8.99 + 1.79X$	0.51**
G6		$Y = -3.43 + 0.69X$	0.40**
Soil population vs time			
Topa Topa		$Y = 1.45 + 1.99X$	0.41**
Duke 7		$Y = -24.53 + 4.01X$	0.50**
G6		$Y = -10.83 + 1.25X$	0.34*
Root weight vs time			
Topa Topa	Uninfected	$Y = -13.05 + 3.76X$	0.63**
	Infected	$Y = 6.89 + 0.23X$	0.35*
Duke 7	Uninfected	$Y = 19.52 + 0.51X$	0.37*
	Infected	$Y = 14.14 + 0.57X$	0.44**
G6	Uninfected	$Y = 9.63 + 1.05X$	0.57**
	Infected	$Y = 5.01 + 0.72X$	0.47**
Shoot weight vs time			
Topa Topa	Uninfected	$Y = -8.82 + 3.69X$	0.80**
	Infected	$Y = 8.81 + 1.06X$	0.46**
Duke 7	Uninfected	$Y = 9.27 + 1.51X$	0.64**
	Infected	$Y = 10.74 + 1.73X$	0.65**
G6	Uninfected	$Y = -7.17 + 3.56X$	0.80**
	Infected	$-0.38 + 2.37X$	0.66**

[a] There are 40 degrees of freedom for each equation.
[b] Correlation coefficients (r) are significant at $P = 0.01$ (**) or $P = 0.05$ (*).

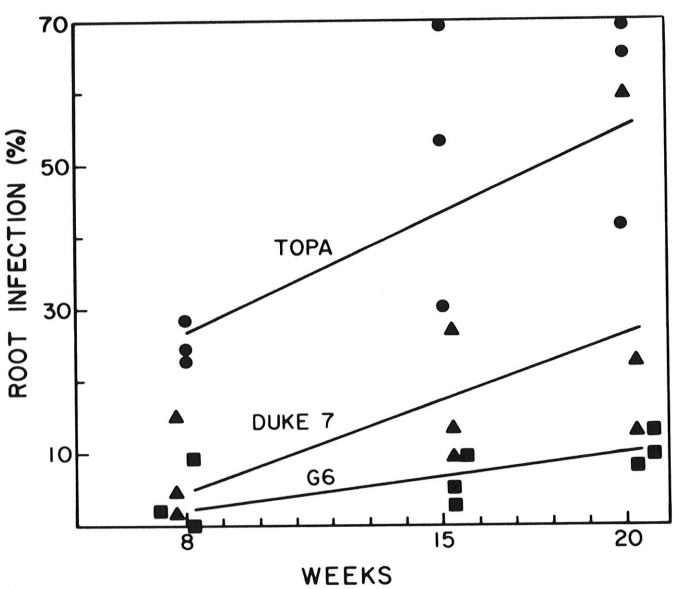

Fig. 1. Regression analysis of the percentage of roots of Topa Topa, Duke 7, and G6 avocado rootstocks infected with *Phytophthora cinnamomi* at 8, 15, and 20 wk after planting in naturally infested soil. Analysis of covariance indicates that regression lines are significantly different ($P = 0.01$). Mean values for each of three experiments are given for each date (● = Topa; ▲ = Duke 7; and ■ = G6).

Propagules in infected root tissue. Since the number of propagules recovered from surface-disinfested roots on dilution plates in root maceration experiments did not differ significantly among experiments, the data were combined for comparison (Table 3). No significant difference was found in the number of internally produced propagules recovered from roots of Walter Hole, Duke 7, and G6. However, significantly more propagules were recovered from detached roots of Walter Hole and Duke 7 infected in culture than from attached roots infected in the greenhouse. There were no significant differences between culture- and greenhouse-infected roots of G6. Mycelia and chlamydospores were observed in macerated preparations of the three rootstocks.

Root growth potential. Root weights of the root-pruned Walter Hole or Topa Topa were not significantly different from the unpruned control after 4 wk, whereas root weights of the root-pruned Duke 7 and G6 rootstocks were significantly greater than those of the unpruned controls (Table 4). Shoot weights were not significantly different in pruned or unpruned treatments.

DISCUSSION

A quantitative comparison was made of disease progress in ungrafted susceptible Topa Topa and resistant Duke 7 and G6 rootstocks. The results confirmed previous field observations (15), namely, that both the Duke 7 and G6 rootstocks were moderately resistant to Phytophthora root rot.

Due to the number of plants required for these experiments, material was obtained from commercial nurseries. Plants used in different experiments often varied in age and state of root development because of variation in propagation techniques and environmental conditions. Therefore, root weights of Topa Topa, Duke 7, and G6 sometimes varied considerably between experiments. Such variation is an inherent difficulty with the avocado system. This does not prevent meaningful data collection when consistent trends are observed in repeated experiments, although direct comparisons between selections are usually impossible.

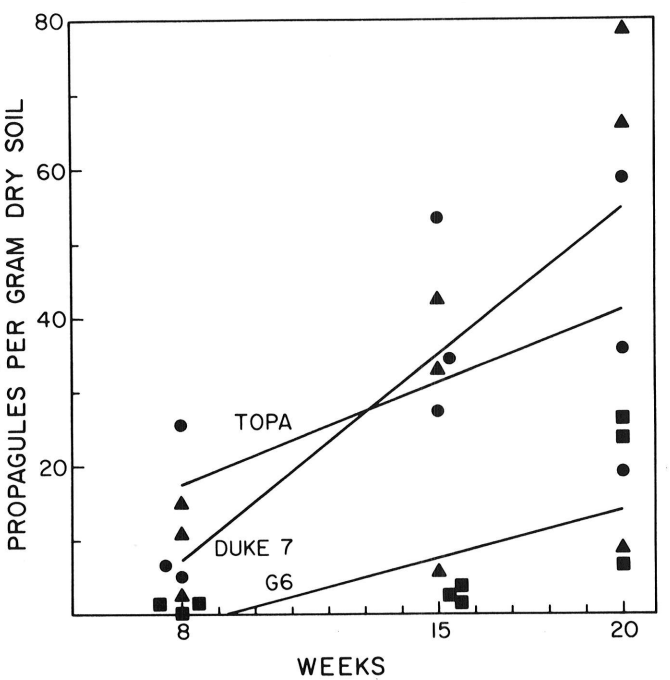

Fig. 2. Regression analysis of the propagules of *Phytophthora cinnamomi* per gram of dry soil recovered from pots containing Topa Topa, Duke 7, or G6 avocado rootstocks at 8, 15, and 20 wk after planting in naturally infested soil. Analysis of covariance indicates significant differences between regression lines of Topa Topa and G6 ($P = 0.01$) and Duke 7 and G6 ($P = 0.05$). Mean values for each of three experiments are given for each date (● = Topa; ▲ = Duke 7; and ■ = G6).

The observed differences in the soil populations of *P. cinnamomi* and root infection suggested that separate types of resistance mechanisms might operate in Duke 7 and G6. Rates of population increase and final population levels in soil were similar for Duke 7 and Topa Topa, reaching 55 and 42 ppg, respectively, after 20 wk. With G6, the soil population increased at a slower rate and reached a final level of 14 ppg. Root infection of G6 was significantly less than that of Duke 7, which correlated with the slower increase in soil populations. These results demonstrated that infected roots of Duke 7 supported a higher capacity for sporulation of *P. cinnamomi* than did infected roots of Topa Topa and G6. Since the same levels of internally produced propagules were found in susceptible and resistant rootstocks, sporangia produced on root surfaces are a likely source of the differences. In some comparisons of eucalypts susceptible and resistant to *P. cinnamomi*, more sporangia were observed on external root surfaces of the resistant species (5,6).

TABLE 2. Relationship of the reduction in root weight to the amount of root infection of susceptible Topa Topa and resistant Duke 7 and G6 avocado rootstocks at 8, 15, and 20 wk after planting into soil infested with *Phytophthora cinnamomi*

Time (wk)	Reduction in root weight (%)[x]			Root infection (%)[y]		
	Topa Topa	Duke 7	G6	Topa Topa	Duke 7	G6
8	48.5[z]	22.5	40.0	25.5	8.0	3.4
15	76.0	18.4	37.2	45.5	17.9	7.1
20	81.0	16.1	36.3	59.9	25.0	9.7

[x] Percentage of reduction in dry root weight compared to controls [100 × (uninfected dry root weight minus infected root weight)/(uninfected root wt).].
[y] Percentage of infected roots on individual plants.
[z] Each value represents the average of the means of three experiments.

In our greenhouse experiments, relatively low initial soil populations of *P. cinnamomi* that ranged from 0.3 to 3.1 ppg resulted in severe infection of the susceptible rootstock, as well as significant root infection and root reduction of the resistant rootstocks. These results are similar to the inoculum density-infection relationships of several species of *Phytophthora* with various hosts in artifically and naturally infested soils where an initial inoculum level of less than 1.5 ppg resulted in significant disease (8,10).

The relatively low level of soil populations that developed with G6 suggested that a type of resistance involving restricted infection and sporulation of *P. cinnamomi* might be operating. A microscopic analysis of infection sites would be needed to define components of resistance at this level. A restricted root infection by

TABLE 3. Propagules of *Phytophthora cinnamomi* recovered from roots of three avocado rootstocks infected in culture or in soil in the greenhouse by using a root maceration technique

Rootstock cultivar	Propagules per gram dry root (× 10^4)	
	Soil[x]	Culture[y]
Walter Hole	4.2[z] b	14.3 a
Duke 7	4.9 b	17.0 a
G6	10.6 ab	14.1 a

[x] Infected roots were obtained from greenhouse experiments 20 wk after planting in soil infested with *P. cinnamomi*. Data are averages of two experiments.
[y] Excised roots were inoculated with zoospores (10^3 per root tip) and incubated for 4 days before root maceration. Data are averages of four experiments.
[z] In rows and columns, values with different letters are significantly different ($P = 0.05$) according to Duncan's multiple range test.

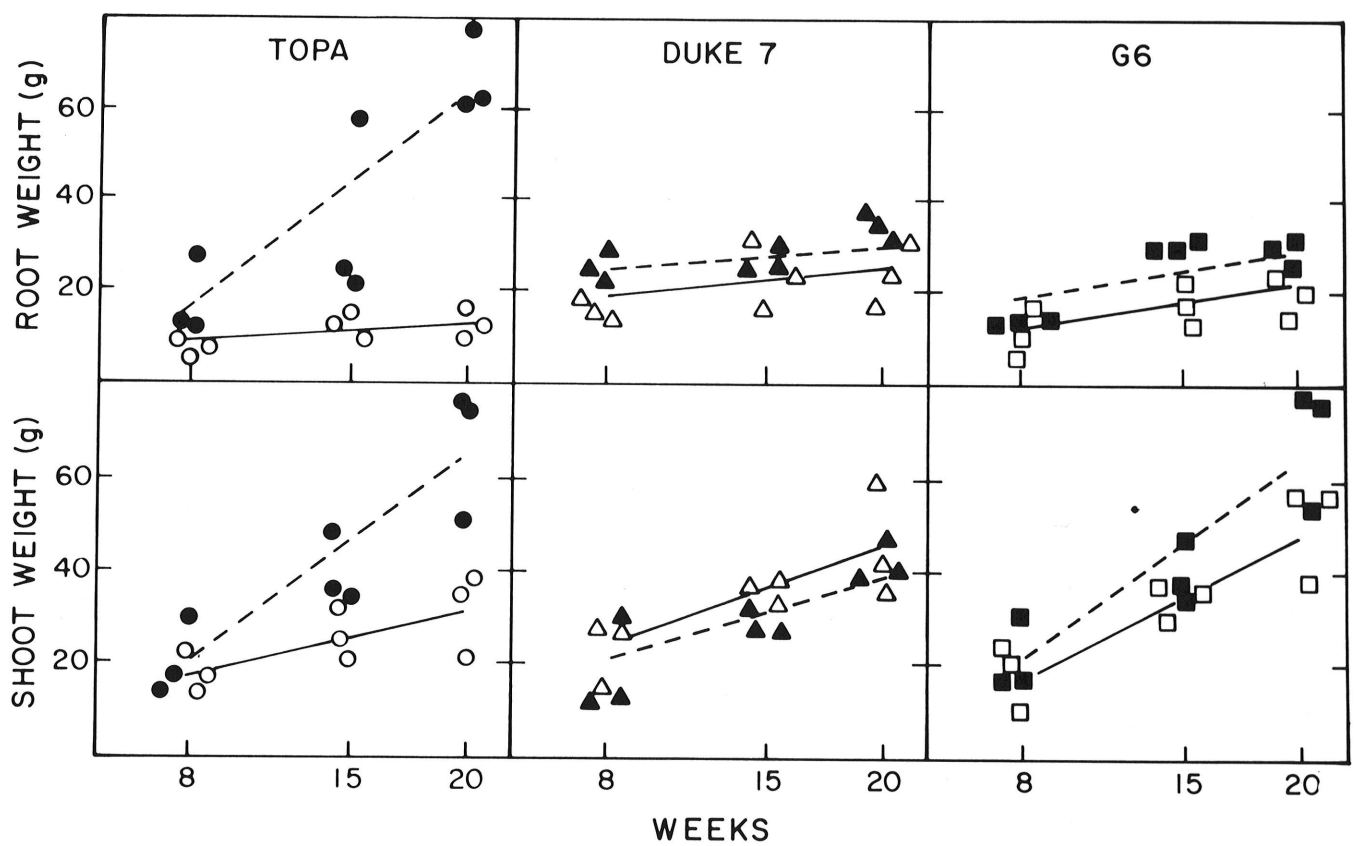

Fig. 3. Regression analysis of root and shoot weights of Topa Topa, Duke 7, and G6 avocado rootstocks 8, 15, and 20 wk after planting in soils infested (o, Δ, □) and uninfested (•, ▲, ■) with *Phytophthora cinnamomi*. Regression lines within each box are significantly different from each other ($P = 0.05$) by use of analysis of covariance or adjusted means. Mean values for each of three experiments are given for each date (• = Topa; ▲ = Duke 7; and ■ = G6).

TABLE 4. Effect of root pruning on dry root weights of susceptible seedlings of cultivars Walter Hole and Topa Topa, and resistant cuttings of cultivars Duke 7 and G6, 4 wk after treatment

Expt. no. and root pruning %	Dry root weights (g)			
	Susceptible		Resistant	
	Topa Topa	Walter Hole	Duke 7	G6
Experiment 1[w]				
0[x]		2.7 a[y,z]	1.1 b	2.0 b
50		2.3 a	3.4 a	3.4 a
Experiment 2				
0	2.4 a		13.5 b	10.5 b
50	2.9 a		22.5 a	13.7 a

[w] Two experiments were conducted using two susceptible rootstocks.
[x] At planting, 0 or 50% of each root system was excised longitudinally. Treatments contained seven or eight replications.
[y] Dry root weight in grams.
[z] Data in columns within each experiment followed by the same letter are not significantly different from each other according to Duncan's multiple range test ($P = 0.05$).

P. cinnamomi, defined as hypersensitivity, has been reported in only one instance, with *Acacia pulchella* (12).

As measured by differences in their shoot and root weights when planted in soil infested with *P. cinnamomi*, the resistant rootstocks were much less susceptible to root rot, than was Topa Topa. A comparison of the amount of root infection with the reduction in root weight provides another basis for hypothesizing that different resistance mechanisms may operate in Duke 7 and G6. Duke 7 sustained a relatively high amount of root infection, yet showed no significant reduction in root weight compared to uninfected controls. Conversely, G6 sustained a lower amount of infection, but the reduction in root weight was much more pronounced than for Duke 7. Topa Topa exhibited both high levels of root infection and a reduction in root weight.

Root growth potential would appear to be another component of the field resistance to avocado root rot. In the absence of *P. cinnamomi*, both Duke 7 and G6 had greater root growth capacities than the susceptible rootstocks, Walter Hole and Topa Topa. Infected G6 plants demonstrated a significantly greater rate of root growth than Topa Topa, whereas the rate of root growth of infected plants was not significantly different between Topa Topa and Duke 7 or G6 and Duke 7. Greater root growth potential has been correlated with increased resistance to *P. cinnamomi* among *Eucalyptus* spp. (2,6), and to *P. citrophthora* among *Citrus* spp. (3). Field (general) resistance in several hosts would appear to be related more to agronomic characters, than to specific genetic interactions directly involving restriction of pathogen development (4,11).

Similar numbers of propagules of *P. cinnamomi* were recovered from roots of both resistant and suceptible rootstocks infected in culture and in soil. Other reports indicate similarities in tissue penetration and colonization by *P. cinnamomi* in both resistant and susceptible *Persea* spp. (7) and *Eucalyptus* spp. (2,9,13). Since propagules within avocado roots are thought to serve as inoculum for additional root infection (15), quantification of propagules within roots might prove useful for ecological and epidemiological investigations.

The level of *P. cinnamomi* recovered from soil in these experiments was generally higher than that normally recovered from diseased avocado trees in the field (M. K. Kellam, *unpublished*). This difference is most likely due to the restricted size of the container used to grow these rootstocks. The high populations of *P. cinnamomi* that were generated should exert a severe disease pressure on the rootstocks, making this a good system for the screening of resistant material.

The amount of root infection, apparent infection rate, and root growth potential proved to be useful parameters in quantitative comparison of resistance of avocado rootstocks. Our results indicate the possibility that Duke 7 might actually support higher populations of *P. cinnamomi* than would a susceptible rootstock such as Topa Topa, thereby acting as a reservoir of inoculum for infection of other individuals.

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