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THE EFFECT OF ROOT INFECTION BY PHYTOPHTHORA CINNAMOMI AND SOIL OXYGEN CONTENT ON THE CONCENTRATIONS AND TOTAL AMOUNTS OF NUTRIENTS IN AVOCADO PLANTS (PERSEA AMERICANA MILL)

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Avocado root rot was first reported by Tucker (8) in Puerto Rico in 1927, and has been present in California for many years. Early references to "water injury" to avocado trees in California in the 1920's probably refer to what is now known as Phytophthora root rot. In 1942, Wager (10) first reported the relation of *Phytophthora cinnamomi* to avocado "decline" in California.

The role of the fungus, *P. cinnamomi,* in avocado root rot was demonstrated in California in the late 1940's and early 1950's by Zentmyer and Klotz (12) and by Zentmyer (11). The role of restricted soil drainage or excess water in avocado root rot has been recognized for many years (1, 10, 11, 13, 14). Soils with poor internal drainage provide a favorable environment for the development of water molds, and also may have reduced oxygen availability for roots. Usually, under such conditions, avocado root rot is a serious problem (11). In soils with poor drainage oxygen diffusion from the atmosphere is reduced by a factor of 10,000 (7). Zentmyer (11) suggested that excess water is more important because of its effects on the fungus than because of any harmful effect on the host. The fungus needs water to form sporangia and zoospores and to permit spore mobility and infection. Klotz *et al.* (3) found that a reduction in aeration of orange seedling root environment decreased the rate of root production, stem height, and water use, but did not affect the rate of root decay or rate of increase in weight of stem and leaves. Curtis and Zentmyer (2) conducted experiments in solution cultures which were inoculated with *P. cinnamomi* and treated with differential O_2 levels. Root injury due to the fungus was more rapid and severe under the highest O_2 treatment. Valoras *et al.* (9) also suggested that reduced soil oxygen supply in itself is not the primary cause of severe root damage in the field but that the action of *P. cinnamomi* in the roots is the most important factor. From this point of view, such results indicate that *Phytophthora* damage should be greater on a well-drained rather than on a poorly-drained soil because the rate of O_2 supply would be greater in the well-drained soil. This, however, has not been observed in the field. Other factors, such as nutrition of plants, or water must, therefore, be involved.

The effects of *P. cinnamomi* on root rot, nutrient uptake, translocation, and total amounts of nutrients taken up by the plant under differential soil oxygen supply levels are, therefore, of considerable interest. This study evaluated the main effects of *P. cinnamomi, soil* oxygen levels, and their interaction, on the dry weight of plant parts produced, nutrient concentrations in the leaves, stems, and roots, and the total amounts of nutrients taken up by avocado plants growing under these differential soil treatment conditions.

MATERIALS AND METHODS

Uniform avocado seedlings (*Persea americana* Mill.) var. Topa Topa were transplanted into Fallbrook sandy loam in acrylic containers 46 cm deep and 22 cm in diameter. Before seedlings were transplanted, the lower one-third of 16 soil columns was inoculated with isolates of *P. cinnamomi* using sterlized alfalfa stems in which the fungus was growing. Sixteen other soil columns were left uninoculated. These containers were tightly sealed with plastic lids which had openings for entrance and exit of gases and for placement of tensiometers.

One tensiometer cup was placed at a soil depth of 15 cm and the other at 40 cm. The soil-water regime for each soil column was based on soil suction values measured with the two tensiometers. The soil column was watered with 0.5-1.0 liter of either deionized water or single strength Hoagland solution whenever the tensiometer at the 15 cm depth indicated a soil suction of 20 centibars (cb). This amount of liquid added, lowered the soil suction at the 40 cm tensiometer cup to approximately 3 cb. Soil-root temperature was maintained at 25 ±2°C in controlled constant temperature tanks. Above ground parts of seedlings were exposed to a controlled greenhouse day-night air temperature range of 19 to 39°C during the growing period. The greenhouse was equipped with evaporative coolers and activated charcoal filters to remove air pollutants. When seedlings were approximately 6 months old, three oxygen treatments were imposed on the soil-root environment by flowing (air): (a) 21% O_2, (b) gases with 10% O_2 and 90% N_2 or (c) 40% O_2 and 96% N, over the soil surface for 40 days. The two sets of avocado seedlings—inoculated and uninoculated—at the three oxygen levels were replicated four times.

After termination of this experiment, the avocado seedlings were cut off at the top of the tap root. Leaves, stems, and roots were separated, washed, dried and ground. Methods of sample preparation for nutrient analysis were as previously described (4). Data obtained from tissue analyses have been analyzed statistically.

RESULTS

Phytophthora Effects. The dry weight of leaves, stems, and roots from infected plants was significantly lower than that from non-infected ones (Tables 1 and 2). Leaves of fungus-infected plants showed an increase in N, K, Na, and Cu, and a decrease in P, Mg, Mn, and Fe concentrations as compared to the non-infected plants. Concentrations of Ca, Cl, and Zn in leaves were not influenced measurably by the presence of *P. cinnamomi* in the avocado root systems. Presence of the fungus in the soil system produced higher concentrations of N, P, K, Ca, Mg, Na, Cl, Cu and Fe in plant stems than a non-infected root system. Zinc and Mn concentrations in infected plant stems were not changed. Roots of infected plants contained lower concentrations of P, Mg, Na, Cl, Zn, Mn, and Fe, higher N and Cu, but K and Ca concentrations remained unchanged (Tables 1 and 2).

Regardless of changes in concentrations of various nutrients found in infected plant tissue, the total individual nutrient uptake per plant was lower than that in the non-infected plants. It was found, without exception, that the presence of *P. cinnamomi* in the root system definitely affected nutrient uptake by the plant. Non-infected avocado plant root systems were used as the criterion for assessing root damage by fungi in infected soil systems.

The data showed (Tables 1 and 2) that the presence of *P. cinnamomi* in the root systems resulted in changes in nutrient concentrations in leaves, stems, and roots, and also in the total nutrient uptake by the plant.

Soil Oxygen Effects. Neither dry weights of leaves, stems, and roots nor the nutrient concentrations and the total amounts of nutrients per plant were influenced measurably by the soil oxygen treatments. The data of the main soil oxygen effects, therefore, on the dry weights of plants and nutrient concentrations in avocado seedlings were not presented in this paper. Although no significant main effects of soil oxygen on the nutrient concentrations and the total amounts of nutrients per plant were shown, there were several significant interactions between *P. cinnamomi* root infestation and soil oxygen levels on the concentrations of N, P, K, Mg, and Na on avocado leaves. Reduced soil oxygen levels decreased the N, K, Mg, and Na concentrations in the leaves of plants which were not inoculated with *P. cinnamomi.* In the presence of fungus in the root systems, the reduced soil oxygen increased the N, K, Mg, and Na concentrations in the leaves (Table 3). When the soil oxygen level was reduced from 21 to 4% in non-inoculated plants, the concentration of P in the leaves was reduced, whereas, the presence of *P. cinnamomi* in the root system under reduced soil oxygen levels did not measurably affect P concentration in the leaves.

DISCUSSION

The decrease or increase in the nutrient concentrations in plant tissues was related to the presence of *P. cinnamomi* in the root system. Nutrient uptake and translocation from infected roots to stems and leaves were also affected by the presence of fungus in roots. These findings agree with those reported earlier on citrus and avocado seedlings (3, 6, 7).

Higher concentrations of N in the leaves, stems, and roots of infected plants were associated with lower amounts of dry weight produced. The lower amount of dry weight per plant growing under the same fertilizer regime resulted in higher nutrient concentrations in the tissues. This finding agrees with previous observations on avocado seedlings (5). The presence of *P. cinnamomi* in the root zone does not directly increase the uptake of N. Measurement of the total amount of N taken up by the plant showed that the amount was substantially lower in the infected than the non-infected plant.

The accumulation of P in stems of infected plants was very pronounced. Phosphorus was taken up by the roots and translocated to the stems. The accumulation of P in stems of infected plants indicated that P translocation to the new top growing points was inhibited.

Sodium and Cl concentrations in roots of infected plants were lower than in non-infected, but substantially higher in stems and leaves. This indicated that, in the case of root injury, there was increased translocation of Na and Cl from roots to tops of avocado plants. This phenomenon has been observed in previous experiments (5) on avocados. When citrus or avocado plant roots are injured either by soil microorganisms or by some adverse factors such as lack of soil oxygen or too much soil moisture, Na and Cl was excessively translocated to the tops of the plants and in such cases may reach toxicity levels in plants even though the soils themselves are not excessively high in Na and Cl. It appears that the entry of Na and Cl into injured roots is a passive one.

Roots and tops of infected avocado seedlings contained lower concentrations of Mn than did non-infected ones. Injured roots either were not able to absorb the available Mn from the soil solution or the availability of Mn was decreased by activity of the fungi.

Although the total uptake of Cu and Fe by infected plants was lower, the reduction in plant dry weight was not due to Cu and Fe deficiencies. The concentrations of Cu and Fe in leaves of infected plants was adequate for normal plant growth. The reduction in dry weight of infected plants was attributed to *P. cinnamomi* damage to the root system and a consequent reduction in the component manufacturing capability of roots.

It has been established previously that avocado roots and plants die if oxygen content in either soil or solution cultures is too low (9). Valoras *et al.* (9) found that avocado plants growing under a 1 % oxygen treatment wilted and died. All of the plants grown under a 2% oxygen treatment had some wilt and several plants died. None of the plants growing under a *5%* oxygen treatment died, but a considerable amount of tip burn occurred on the leaves. In soil surveys in connection with avocado root rot (1), both low soil oxygen supply and *P. cinnamomi* infestation of the soil were associated with root rot. Since both low soil oxygen and *Phytophthora* have been demonstrated to be harmful to avocados, it is not immediately apparent which is the dominating factor contributing to root rot. Very likely low soil oxygen can decrease tree growth and production, but *P. cinnamomi* is necessary for severe tree damage.

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TABLE 1. EFFECTS OF PHYTOPHTHORA SPP. ROOT INFESTATION ON DRY WEIGHT OF AVOCADO PLANT, MACRONUTRIENT CONCENTRATIONS IN LEAVES, STEMS, AND ROOTS, AND ON THE TOTAL AMOUNTS OF NUTRIENTS/PLANT[z]

	(–) *Phyt.*	(+) *Phyt.*	*Level of Sign.*	*C.V.*
Dry wt (g)				
Leaves	52.95	6.42	***	28
Stems	390.08	1.71	***	36
Roots	26.71	2.71	***	27
Total/plant	118.74	10.84	***	29
Nitrogen				
Leaves (%)	2.20	2.35	*	9
Stems (%)	0.87	1.84	***	29
Roots (%)	1.18	1.44	**	18
Total/plant (g)	1.79	0.21	***	21
Phosphorus				
Leaves (%)	0.189	0.144	***	8
Stems (%)	0.177	0.460	***	56
Roots (%)	0.235	0.185	**	21
Total/plant (g)	0.229	0.020	***	26
Potassium				
Leaves (%)	0.70	0.83	**	13
Stems (%)	0.54	1.45	**	83
Roots (%)	0.62	0.62	NS	34
Total/plant (g)	0.74	0.08	***	22
Calcium				
Leaves (%)	2.10	2.13	NS	14
Stems (%)	0.26	1.64	***	62
Roots (%)	0.40	0.38	NS	24
Total/plant (g)	1.30	0.17	***	24
Magnesium				
Leaves (%)	0.70	0.61	*	14
Stems (%)	0.17	0.71	***	64
Roots (%)	0.33	0.18	***	21
Total/plant (g)	0.52	0.05	***	26
Sodium				
Leaves (%)	0.016	0.120	***	63
Stems (%)	0.032	0.147	***	78
Roots (%)	0.325	0.197	***	19
Total/plant (g)	0.104	0.013	***	19
Chloride				
Leaves (%)	0.099	0.099	NS	46
Stems (%)	0.030	0.127	***	77
Roots (%)	0.366	0.165	***	19
Total/plant (g)	0.160	0.012	***	29

[z]*Each value is a mean of 16 individual determinations*
*=*Significant at the 5% level*
**=*Significant at the 1% level or higher*
NS=*Indicates that differences between means are not significant*

TABLE 2. EFFECTS OF PHYTOPHTHORA SPP. ROOT INFESTATION ON MICRONUTRIENT CONCENTRATIONS IN LEAVES, STEMS, AND ROOTS, AND ON TOTAL AMOUNTS OF NUTRIENTS/PLANTS[z]

	(–) Phyt.	*(+) Phyt.*	*Level of Sign.*	*C.V.*
Zinc				
Leaves (ppm)	29.10	28.70	NS	15
Stems (ppm)	15.90	18.40	NS	24
Roots (ppm)	33.70	21.60	***	19
Total/plant (mg)	3.04	0.27	***	32
Manganese				
Leaves (ppm)	37.30	22.80	***	21
Stems (ppm)	5.30	7.40	NS	53
Roots (ppm)	15.00	7.10	**	56
Total/plant (mg)	2.55	0.21	***	28
Copper				
Leaves (ppm)	3.10	4.90	***	13
Stems (ppm)	1.10	4.50	***	19
Roots (ppm)	4.40	10.40	**	72
Total/plant (mg)	0.33	0.06	***	26
Iron				
Leaves (ppm)	50.30	27.60	***	18
Stems (ppm)	25.60	94.60	***	71
Roots (ppm)	755.00	238.00	***	33
Total/plant (mg)	23.64	1.24	***	31

[z]See footnotes, Table 1.

TABLE 3. INTERACTIONS AMONG PHYTOPHTHORA SPP. ROOT INFESTATION AND SOIL OXYGEN CONTENT ON THE CONCENTRATIONS OF N, P, K, Mg AND Na IN AVOCADO LEAVES[z]

Soil-O_2 level	Per cent on dry wt basis: N		Mg		Na	
	(–)Phyt.	(+)Phyt.	(–)Phyt.	(+)Phyt.	(–)Phyt.	(+)Phyt.
21%	2.34	2.25	0.745	0.567	0.017	0.072
10%	2.05	2.44	0.662	0.654	0.014	0.168
Level of Signif.	**		*		**	

Soil-O_2 level	Per cent on dry wt basis: P		K		Mg	
	(–)Phyt.	(+)Phyt.	(–)Phyt.	(+)Phyt.	(–)Phyt.	(+)Phyt.
21%	0.202	0.145	0.72	0.67	0.752	0.590
4%	0.177	0.143	0.68	0.98	0.655	0.632
Level of Signif.	*		**		*	

[z]Each value is a mean of 8 individual determinations;

**=significant at the 5% level;*

***=significant at the 1% level.*