Proceedings of the
AMERICAN SOCIETY FOR HORTICULTURAL SCIENCE
1967 90:67-76

Oxygen Diffusion, Water, and *Phytophthora cinnamomi* in Root Decay and Nutrition of Avocados[1]

L. H. STOLZY, G. A. ZENTMYER, L. J. KLOTZ, and C. K. LABANAUSKAS,[2]
University of California., Riverside

Abstract. Addition of *Phytophthora cinnamomi* to soil resulted in significant root decay and changes in the mineral nutrient concentrations of the plant parts. The degree of root decay was also significant in water-saturated soils in the presence or absence of the fungus. The high water content also appeared to have an adverse effect on the establishment of the fungus in the zoospore-germ tube stage. Limited oxygen supply in the root zone was the most severe soil physical factor in both the growth and decay of roots. Plants growing in soils with oxygen diffusion rates of 0.17 μg cm^{-2} min^{-1} and less had 44 to 100% of their root systems in a state of decay.

INTRODUCTION

IN soils with poor drainage, destruction of avocado roots by *Phytophthora cinnamomi,* Rands, is severe (12, 14). Zentmyer and Bingham (13) suggested that the primary role of excess soil water is that it provides a medium in which *P. cinnamomi* can produce its spore stages and in which the motile spore stage can be disseminated and infect roots. Saturated soils not only provide a better environment for the development of water molds but also reduce the oxygen diffusion into soils by a factor of 10,000 (7). Valoras et al. (11), however, suggest that reduced oxygen supply in itself is not the primary cause of severe tree damage in the field but that the action of *P. cinnamomi* on the roots is the most important factor. The fact that root injury in solution has been shown to be more severe in the presence of the fungus at higher oxygen concentrations would indicate a root decay interaction between saturated soils and the fungus (3).

The reason for this study was to compare results obtained on avocado with those of other studies involving water and aeration treatment on citrus plants.

MATERIALS AND METHODS

Seven-week-old uniform avocado *(Persea americana* 'Mexicola') seedlings were transplanted into Fallbrook sandy loam contained in 1-liter glass cylinders painted on the outside. The soil was free from *Phytophthora cinnamomi.* An unpainted vertical strip 1 cm wide was covered with black tape that could be removed for root observations during the experiment (Fig. 1). Two experiments were conducted, the first experiment was to study mainly the influence of *P. cinnamomi* and irrigation on the nutrition of the plant and the degree of root decay. The second experiment was designed to

[1]Received for publication September 21, 1966. Paper No. 1771, University of California Citrus Research Center and Agricultural Experiment Station, Riverside. Supported in part by NSF Grant No. GB-84.
[2]The authors acknowledge the technical assistance of S. M. Mircetich and T. E. Szuszkiewicz.

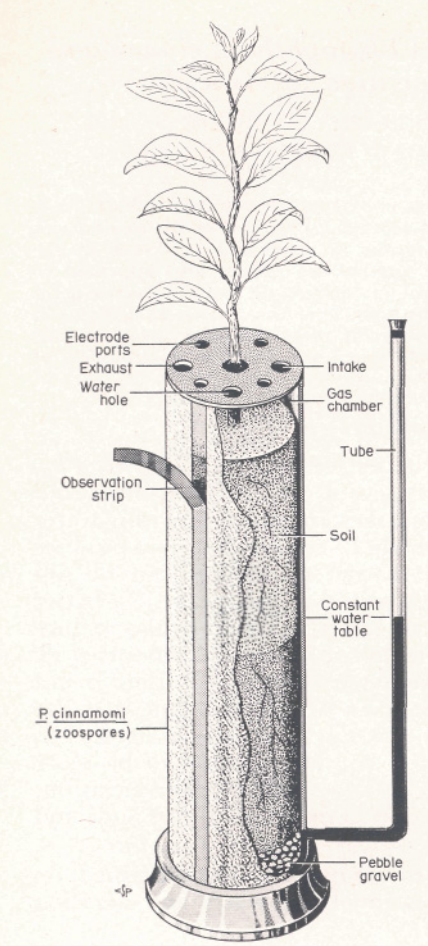

Fig. 1. Plant-container arrangement for studying effects of soil, water and aeration on plant growth and root decay of Mexicola avocado seedlings. Container is an example of treatment D with a water table.

study the interaction of the fungi, irrigation and soil oxygen supply on plant response, and root decay. The study was done in a greenhouse maintained at about 28C during the day and 24C at night. The evaporative coolers were equipped with activated charcoal filters to remove air pollutants. The plants were watered with deionized water and occasionally with nutrient solution to wet the entire soil column without causing outflow at the bottom. When the seedling roots had grown almost to the bottom of the soil columns (approximately 2.5 months) half of the soil columns were infested with 10 ml of zoospore suspension of *P. cinnamomi* injected into the lower one-third of the soil column (Fig. 1). Four days later, watering and aeration treatments were started. The watering treatments were replicated 4 times in each of 2 separate experiments. Soil aeration treatments, replicated 4 times, were applied in only the second treatment. In both experiments, treatments were continued for 35 days. Irrigation treatments consisted of the following: A) check, in which the soils were watered to an average moisture content of 19% on oven-dry basis using the weighted pot methods to determine the amount of water used by the plant over a three-day period. This was the

condition during the period when the plants were becoming established; B) the entire soil column was saturated for an 8-hour period every 10 days by introducing water at the bottom opening until the soil column was saturated and then allowing it to drain at the end of 8 hours; C) the entire soil column was saturated for a few minutes every 4 days and then drained; D) a water table was maintained half-way up the soil column (water was applied at the top of the column to rewet the top soil as it was needed).

Soil aeration was varied by having sealed lids with intake and exhaust ports through which gas of different oxygen concentrations were flowed over the soil surface from a distribution and mixing manifold described in more detail by Stolzy and Letey (8). The two levels of oxygen were high level with oxygen in air at a partial pressure of 152 mm Hg; low level with air and nitrogen to supply oxygen at 16 mm Hg.

The oxygen concentration over the soil surface changes the oxygen supply in the soil as reported earlier by Stolzy et al. (8). The oxygen condition in the root zone was characterized by measuring oxygen diffusion rates (ODR) in the soil with a platinum electrode at the termination of the experiment (6). Several factors influence the ODR in soils: oxygen gradient, water content, pore space, compaction, and diffusion coefficient in the soil solution. The ODR value measured in this way is similar to the ODR value which influences root and soil organisms.

During the treatment period, condition of plant tops was rated as a probable indication of the stage of root decay on a scale of 0 to 5. Zero rating meant healthy normal plants. Ratings from 1 to 5 meant a progressive deterioration in the plant and were based on general appearance of shoot, presence of new growth, size of leaves, chlorosis and wilt. A rating of 5 indicated a dead plant. At the termination of the experiments, roots were separated from shoots, and soils. Both plant parts were handwashed in tap water containing 0.1% detergent and rinsed in demineralized water. The percentage of root decay was then estimated based on visual observation of decay of the cortex. The plant parts were then dried in a forced-draft oven at 60 C for 48 hours. In the first experiment, plant materials were ground and macro- and micronutrient analyses made as described by Labanauskas et al. (5). Soils from all columns were checked for the presence of *P. cinnamomi* by culturing roots and using the fruit test (14).

RESULTS

Nutrients: It has been of great interest to research workers in the field of plant nutrition and plant pathology to find out to what degree various irrigation levels and infestation of the plant-growing medium of fungi would affect the nutrient concentrations in the roots and shoots of the avocado plants. The data in Table 1 clearly show that differential irrigation and infestation with *P. cinnamomi* of the soil system caused changes in root decay and nutrient concentrations in the roots and shoots of avocado tissue.

Infection of the root system by the fungus substantially increased the root decay (155%) as compared with the values of root decay obtained from the noninfected seedlings (Table 1). Infected roots contained higher concentrations of N, Ca, and B (30, 37, and 52%, respectively) and lower concentrations of K (19% less) as compared with the values obtained from the analogous samples of noninfected roots. The presence of the fungus in the root system was associated with concentrations of Mn, B, and Fe in the shoots. The concentrations of Mn and B in the shoots of the infected seedlings were

decreased by 27 and 18%, respectively, whereas Fe was increased by 27% as compared with the control treatment values.

Table 1.—Influence of *Phytophthora cinnamomi* and irrigation on root decay and mineral concentrations in dry matter of roots and tops (first experiment).

Treatments	Macronutrients							Micronutrients			Root decay
	N	P	K	Ca	Mg	Na	Cl	Mn	B	Fe	
	%	%	%	%	%	%	%	ppm	ppm	ppm	%
Roots											
Phytophthora[a]											
Absent	0.69	0.11	0.82	0.19	0.18	0.09	0.09	109	32	1066	18
Present	0.90	0.11	0.66	0.26	0.15	0.09	0.08	111	49	1225	46
Irrigation[b]											
A Check	0.82	0.12	0.83	0.22	0.17	0.10	0.06	65	43	916	16
B Saturated every 10 days	0.74	0.12	0.77	0.22	0.19	0.07	0.09	65	34	905	35
C Saturated every 4 days	0.82	0.11	0.74	0.22	0.16	0.08	0.09	82	38	1000	35
D Water table	0.78	0.09	0.61	0.23	0.15	0.12	0.09	227	44	1760	50
Shoots											
Phytophthora[a]											
Absent	0.81	0.09	0.66	0.63	0.29	0.01	0.04	82	50	33	
Present	0.87	0.08	0.70	0.59	0.28	0.01	0.04	60	41	42	
Irrigation[b]											
A Check	0.92	0.09	0.76	0.61	0.29	0.01	0.04	55	44	30	
B Saturated every 10 days	0.77	0.08	0.66	0.61	0.30	0.01	0.04	53	53	33	
C Saturated every 4 days	0.85	0.09	0.71	0.61	0.30	0.01	0.04				
D Water table	0.82	0.07	0.60	0.60	0.26	0.01	0.05	104	36	44	

[a]Each value is a mean of four individual determinations from material composited from four replications.
[b]Each value is a mean of two individual determinations from material composited from four replications.

Irrigation effects on the nutrient concentrations in avocado seedling roots and tops are presented in Table 1. Irrigation treatment D (water table) had the most influence upon the root decay and mineral nutrient concentrations in the roots and tops of the avocado seedlings as compared with these values of similar plant tissue found in the avocado seedlings irrigated according to the treatment A (check). Root decay was 212% higher in the seedlings receiving irrigation treatment D as compared to seedlings in treatment A.

In treatment D, the concentrations of P and K in the roots were decreased by 25 and 26% respectively, whereas Na, Cl, Mn, and Fe concentrations were increased by 20, 50, 249, and 92%, respectively, as compared with the values found in the roots of the control treatment seedlings. In the shoots of the same plants of treatment D, the concentrations of P and K were decreased by 22 and 21%, respectively whereas Mn and Fe were increased by 89 and 46%, respectively, as compared with the values of the analogous material obtained from the control treatment seedlings. Plants in saturated soils with a high degree of root decay had an effect on the mineral concentrations of plants similar to effects observed when *P. cinnamomi* was present which also caused similar amounts of decay. The high concentration of Mn in the plant tissue of C and D treatments is due to an increase in soluble Mn ions in the soil. The higher water content in the soil caused a deficiency of oxygen and so reduced Mn to the more readily available manganous form. Iron is also reduced in the soils where oxygen becomes a limiting factor, and therefore, becomes more available to the plants.

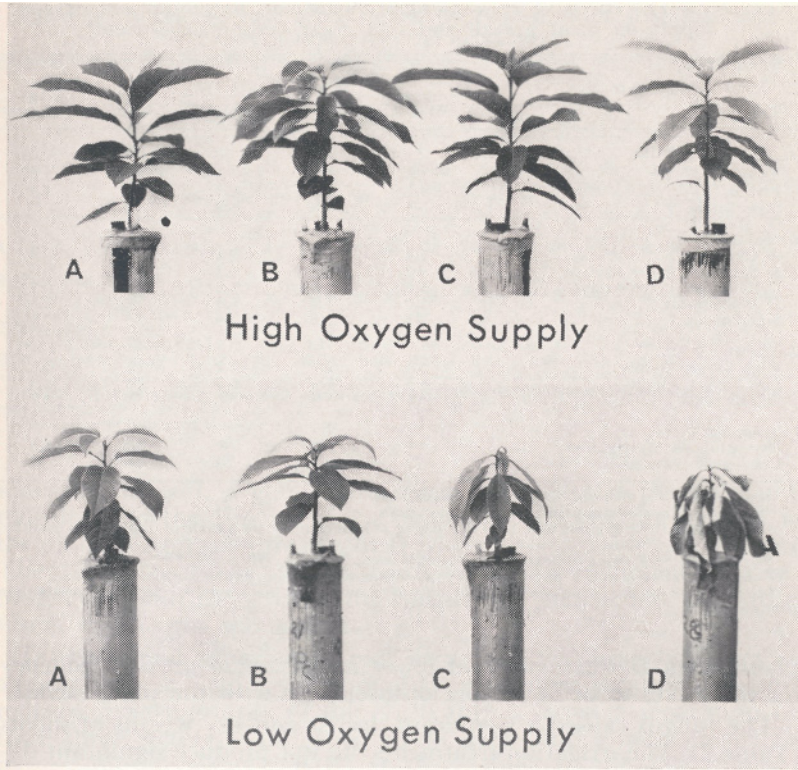

Fig. 2. Shows one average plant from each treatment replication. The plants in the top row had O_2 concentration at the soil surface the same as air while the bottom row had a reduced O_2 concentration at the surface. The letters refer to irrigation treatments. A) Check, B) Saturated every 10 days, C) Saturated every 4 days, and D) water table. Soils were infested with a zoospore suspension of *P. cinnamomi*.

Plant shoots: The effects of oxygen supply to roots and of irrigation treatments on the tops of established 'Mexicola' avocado seedlings are shown in Fig. 2. These plants were inoculated with *P. cinnamomi.* The noninoculated plants responded similarly to oxygen and irrigation but did not show the same degree of damage, especially for irrigation treatments C and D. In Fig. 2 one can see the effect of a reduced oxygen supply. Minimum plant growth occurred under low oxygen with irrigation treatments A and B, whereas in C and D, the plant did not grow and showed damage. In the high oxygen treatment, all the plants developed new growth and only the plants in the D irrigation treatment showed some damage. The plants from D treatment had fewer leaves and a greater tendency for the leaves to be at a more obtuse angle with the plant stem.

The fungus caused a significant decrease in dry weight of shoots (Table 2). The irrigation treatments did not produce significant differences in dry weight of tops. There was only one highly significant interaction and this was P. *cinnamomi* with irrigation on shoot growth. The interaction between the fungus and irrigation appears to involve the survival of the fungi with different watering treatments. The aeration treatment had a highly significant effect on top dry weight production.

Table 2.—The effects of *Phytophthora cinnamomi,* irrigation, and oxygen supply on plant growth and root decay (second experiment).

Treatments	Dry wt/plant			Root decay	Stage of disease[c]
	Shoots	Roots	Total		
	g	*g*	*g*	%	
Phytophthora[a]					
Absent	5.6	2.0	7.6	42	1.0
Present	5.1	2.0	6.9	55	1.4
Significance	*	NS	NS	*	*
Irrigation[b]					
A Check	5.4	2.0	7.4	39_x	0.4_x
B Saturated every 10 days	5.1	1.9	6.7	46_x	0.8_x
C Saturated every 4 days	5.8	2.1	7.9	37_x	0.9_x
D Water table	5.0	1.9	7.0	72_y	2.6_y
Significance	NS	NS	NS	**	**
Aeration[a]					
High oxygen supply	6.5	2.7	9.2	18	0.1
Low oxygen supply	4.1	1.2	5.3	79	2.3
Significance	**	***	***	**	**
Interactions					
Phytophthora × irrigation	**	NS	*	NS	NS
Coefficient of variability (%)	19	25	20	44	32

[a]Each value is a mean of 32 internal replications.
[b]Each value is a mean of 16 internal replications.
[c]Numerical rating of plant tops as to the degree of root damage on a scale of 0 to 5 (0 = healthy, 5 = dead).
Significance = F value indicates at designated level. * = 5%, ** = 1%, *** = 0.1%.
Subscript letters x and y after mean values indicate statistical populations.
Mean values are statistically significant only if they do not have a subscript letter in common after values.

The stage of the disease based on a rating of the top during the treatment period gave an idea of how the plants respond to the treatments (Table 2). The presence of the fungus had a significant effect on the plants. The most marked effects were caused by irrigation treatment D with the low oxygen supply. Irrigation treatments B and C had intermediate effects when compared to plants in the check treatment.

Roots: There was a very highly significant difference in dry weight of roots between those in the high and low supply of oxygen (Table 2). The effects of limited oxygen supply on root growth appear within a few hours as has been shown in studies reported by Stolzy and Letey (7).

Table 3.—Percentage root decay caused by *Phytophthora,* irrigation, and oxygen supply (second experiment).

Irrigation treatment	Fungus absent						Fungus present					
	High O_2			Low O_2			High O_2			Low O_2		
	ODR[a] at soil depths of		Root decay[b]	ODR at soil depths of		Root decay[b]	ODR at soil depths of		Root decay	ODR at soil depths of		Root decay
	15 cm	30 cm		15 cm	30 cm		15 cm	30 cm		15 cm	30 cm	
			%			%			%			%
A Check	0.33	0.31	2	0.10	0.06	71	0.30	0.37	9	0.13	0.06	74
B Saturated every 10 days	0.54	0.41	3	0.08	0.06	76	0.48	0.37	30	0.21	0.12	74
C Saturated every 4 days.	0.38	0.19	4	0.17	0.10	44	0.52	0.24	6	0.12	0.08	94
D Water table.	0.29	0.10	32	0.08	0.08	100	0.16	0.08	58	0.07	0.06	98

[a]ODR = oxygen diffusion rate in $\mu g\ cm^{-2}\ min^{-1}$ (Average of 20 values at the termination of the experiment).
[b]Averages of four root systems.

Root decay demonstrates what is happening to the plants growing under the different soil conditions. In the first experiment, where soil aeration was only indirectly a factor as related to excess water in the soil, a good comparison between the presence and root decay in the absence of *P. cinnamomi* reported in Table 1 is the result of irrigation

treatment D where a water table was present. The 16% root decay, under the A irrigation treatment, was recorded on plant roots where the fungus was present but very little where the fungus was absent.

In the second experiment, root decay was significantly higher as a result of three factors: presence of *P. cinnamomi,* treatment D, and reduced oxygen supply (Table 2). Table 3 shows a separation of these three factors as influencing root decay and a measure of the oxygen diffusion rate (ODR) at two depths in the soil column. The lower ODR numbers mean lower oxygen supplies. Oxygen diffusion rates of less than 0.20 μg cm^{-2} min^{-1} are generally detrimental to roots (8). Plants growing in soil with fungus and a high oxygen supply, only the D treatment had values as low as 0.19 μg cm^{-2} min^{-1}. Most of the root decay in this treatment was in the lower part of the root system. Where the supply of oxygen was reduced, as indicated by ODR values, root decay was much greater. The same is true where the fungus is present except a still greater percentage of root decay resulted.

The number of recoveries of *P. cinnamomi* from the infested soils in the first experiment was much higher than in the second (Table 4), except for the soil in treatment D which had a low recovery in both experiments.

Table 4.—Recovery of *Phytophthora cinnamomi* from soil columns at termination of experiment and percentage root decay in relation to irrigation treatments for the high oxygen supply treatments.

Irrigation treatments	First experiment								Second experiment							
	Recovery of *P. cinnamomi*[a] *Replication*				*Root decay*[b] *Replication*				Recovery of *P. cinnamomi* *Replication*				*Root decay Replication*			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
					%	%	%	%					%	%	%	%
A Check	+	−	+	−	40	0	40	20	−	+	−	−	5	15	10	4
B Saturated every 10 days	+	+	+	+	70	70	60	40	−	+	−	+	1	30	3	85
C Saturated every 4 days	+	+	+	−	40	95	90	10	−	−	−	−	15	3	2	2
D Water table	−	+	−	−	10	70	30	50	−	−	−	−	45	65	50	70

[a] + indicates *P. cinnamomi* was recovered from the soil column at the termination of the experiment. 40 indicates per cent of total root systems was diseased or dead.
[b] − indicates *P. cinnamomi* was not recovered from the soil column at the termination of the experiment. 20 indicates per cent decay.

DISCUSSION

This would indicate that the fungus in the zoospore and germ tube stage is sensitive to very high soil water conditions as in treatment D. Cook and Flentje (2) showed that spore germination of *Fusarium solani f. pisi* was high in soils containing more than 8.7% water, but that a higher percentage of its germ tubes lysed in soils with a water content above 8.7%. Their study may explain the lack of recovery of the fungus from the soil which was saturated 4 days after inoculation with zoospores, or more likely the inability of the fungus to establish itself sufficiently to form resistant structures in roots at high moisture contents. The higher recoveries of the fungus in the treatments A, B, and C of the first experiment as compared to the second one would suggest conditions for the establishment of the fungus were not the same in the two experiments. This could be a temperature factor or possibly a lower population level in the second experiment.

Even where the fungus was not reisolated from cultures in the high oxygen treatments,

zoospore suspensions appeared to be responsible for additional root decay described in Table 3.

In two aeration studies on citrus (9, 10) it was shown that citrus roots decayed at low levels of oxygen supply. The citrus root, being woody, shows less decay in low oxygen treatments than does the avocado with more fleshy tissue. Citrus roots growing in soil infested with *Phytophthora* continue to grow and remain healthy (9) unless the soil environment is made very unfavorable by a saturated condition (10). A saturated soil could both weaken the root and cause a massive infection due to zoospore production at surfaces where aeration permitted germination and infection. Citrus roots with limited *Phytophthora* infections have the ability to terminate the infection and resume growth once the water recedes and conditions unfavorable for germination and mass infection occur.

Avocado roots seem to be affected initially the same as citrus roots. The major difference is that fleshy avocado seedling rootlets do not have a built-in mechanism to terminate the decay. Infected rootlets continue to decay from the infection back to main lateral roots. One *Phytophthora* infection on a growing avocado rootlet destroys it whereas in citrus a massive infection is necessary for maximum damage. Also, citrus rootlets are produced from damaged roots, which is not usually the case with avocado roots. Older avocado roots will produce new rootlets from uninvaded tissue.

It has been shown in this experiment that three soil factors, also other soil conditions not studied, can cause considerable avocado root decay: presence of *P. cinnamomi,* saturated soil, and low oxygen supply. Under field conditions, one or all can contribute to the decline of a tree. Soil surveys in connection with avocado root decay have shown good correlation between soil types and decay (1, 4).

Root injury by poor subsoil drainage combined with attack by root rotting fungi results in a severe root decay problem. The rate at which an area is infested by *P. cinnamomi* is increased on slopes, where water moving over the soil surface or under the surface spreads the fungus. Control of avocado root rot by cultural methods is much more difficult than is control of citrus root decay.

From this study, it is evident that even though *P. cinnamomi* could be controlled, considerable decay of roots would take place whenever a soil was saturated and (or) oxygen supply in the soil was reduced to a low level for a period of time. In the absence of the fungus, correction of these unfavorable conditions would result in recovery of the roots and of the tree. In the presence of the fungus, root decay can occur over a wide range of oxygen levels, from good to poor aeration, providing suitable moisture conditions are present. Maintenance of suitable moisture conditions for the fungus would be expected to occur primarily under conditions of restricted soil drainage. With avocado, the proper selection of soil types appears to be of utmost importance.

LITERATURE CITED

BURNS, R. M., J. H. MINER, C. D. GUSTAFSON, G. A. ZENTMYER, and W. A. THORN. I960. Correlation of soil series and avocado root rot damage in the Fallbrook area. *Calif. Avocado Soc. Yrbk.* 44:110-113.

COOK, R. J., and N. T. FLENTJE. 1965. Influence of soil water on growth and survival

of *Fusarium solani f. pisi* in the rhizosphere of pea. (Abstr.) *Phytopathology.* 55:1053.

CURTIS, D. S., and G. A. ZENTMYER. 1949. Effect of oxygen supply on Phytophthora root rot of avocado in nutrient solution. *Amer. J. Bot.* 36:471-474.

GOODALL, G. E., D. M. HANSEN, and R. M. BURNS. 1962. Santa Barbara County avocado root rot soil survey. *Calif. Avocado Soc. Yrbk.* 46:63-71.

LABANAUSKAS, C. K., R. C. BAINES, and L. H. STOLZY. 1965. Effects of citrus nematode *(Tylenchulus semipenetrans)* and two levels of water suction on nutrient concentrations in navel orange leaves and roots. *Soil Sci.* 99:367-374.

LETEY, J., and L. H. STOLZY. 1964. Measurement of oxygen diffusion rates with the platinum microelectrode. I. Theory and equipment. *Hilgardia.* 35:545-554.

STOLZY, L. H., and J. LETEY. 1964. Characterizing soil oxygen conditions with a platinum microelectrode. *In* A. G. Norman [ed.] *Advances in Agronomy.* 16:249-279. Academic Press, New York.

_____, and _____. 1964. Measurements of oxygen diffusion rates with platinum microelectrode. III. Correlation of plant response to soil oxygen diffusion rates. *Hilgardia.* 35:567-576.

STOLZY, L. H., J. LETEY, L. J. KLOTZ, and T. A. DEWOLFE. 1965. Soil aeration and root-rotting fungi as factors in decay of citrus feeder roots. *Soil Sci.* 99:403-406.

_____, _____, _____, and C. K. LABANAUSKAS. 1965. Water and aerations as factors in root decay of *Citrus sinensis. Phytopathology.* 55:270-275.

VALORAS, N., J. LETEY, L. H. STOLZY, and E. F. FROLICH. 1964. The oxygen requirements for root growth of three avocado varieties. *Proc. Amer. Soc. Hort. Sci.* 85:172-178.

ZENTMYER, G. A. 1963. Diseases of the avocado, 875-881. *In* Plant Diseases, USDA Yrbk. Agriculture.

_____, and F. T. BINGHAM. 1956. The influence of nitrite on the development of *Phytophthora* root rot of avocado. *Phytopathology.* 46:121-124.

_____, A. L. PAULUS, and R. M. BURNS. 1962. Avocado root rot. *Calif. Agr. Ext. Ser. Circ.* 511 p. 13.