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EFFECTS OF FLOODING AND PHYTOPHTHORA ROOT ROT ON PHOTOSYNTHETIC CHARACTERISTICS OF AVOCADO

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ABSTRACT

Experiments were conducted in the greenhouse to determine the effects of flooding and Phytophthora root rot (caused by *Phytophthora cinnamomi)* on photosynthetic characteristics of seedling and grafted avocado (*Persea americana).* Although this disease and flooding individually reduced several different physiological parameters (net CO_2 assimilation, transpiration, and stomatal conductance for CO_2) when compared to nonflooded, nondiseased controls, these reductions were not always significant. However, reductions in these parameters were always highly significant when plants with root rot were flooded. The combined effects of roct rot and flooding were synergistic and resulted in defoliation and death of plants. When different levels of the pathogen were used to infest soil, disease severity (percent root necrosis) was negatively correlated with the physiological parameters tested, regardless of whether or not plants were flooded. Flooded plants generally stopped assimilating CO_2 after root necrosis exceeded 15%. In contrast, nonflooded plants continued to assimilate CO_2, even when root necrosis approached 90%. Although CO_2 assimilation, stomatal conductance, and transpiration were reduced in these plants, they did not die during the course of this work. However, they exhibited foliar chlorosis, and in extreme cases became partially defoliated. It is suggested that previous damage in south Florida avocado groves which was associated with flooding was due to the interaction of flooding with Phytophthora root rot.

High water tables are found in most areas of Dade County, Florida where subtropical and tropical fruit are grown. Depending on rainfall patterns and the location of a given field, water tables may range to within less than a meter of the soil surface during a given year (20, 24). The close proximity of saturated soil to root systems of some of these fruit crops is a liability due to the increased potential for flooding.

Seasonal flooding in Dade County was common before urban development and the excavation of drainage canals in the area (17). Due to the extensive system of canals which now drains Dade County, flooding is less frequent and generally restricted to periods of excessive rainfall associated with hurricanes and tropical storms. For example, extensive and prolonged flooding occurred during and after tropical storm Dennis in 1981. Water remained above the soil surface in some areas for as long as 5-7

days after this storm, and as a result, certain crops such as avocado (*Persea Americana* Mill.), mamey zapote (*Pouteria sapota* [Jacq.] H. E. Moore & Stern), and papaya (*Carica papaya* L.) were severely affected (C. W. Campbell, personal communication). Flood tolerance varies widely among plant species (15). While some plants may tolerate almost continuous flooding, others die within a relatively short time (12). Ruehle (24) suggested that avocado was naturally intolerant of flooding.

Phytophthora root rot is an important problem in most areas in which avocado is grown. This disease is incited by *Phytophthora cinnamomi* Rands, and causes substantial damage in the Eastern (6, 21) and Western (5, 27, 31, 33) Hemispheres. Root rot is most severe in water logged or poorly drained soil (5, 33). In California, healthy avocados withstood flooding for 9 days with no apparent ill effect, while avocados infected with *P. cinnamomi* died when flooded for 2 or more days (32, 35). Similar work has not been conducted in the calcareous soils (Rockdale and less frequently Rockland) found in avocado production areas in Bade County.

The stomatal behavior of plants is frequently changed by disease (1, 2). Although Davison and Tay (7) and Duniway (9) detected no differences in stomatal conductance between infected and noninfected plants in the *P. cinnamomi/jarrah* (*Eucalyptus marginata* Donn ex Sm.) and *P. cryptogea* Pethy. & Laff. /safflower (*Carthamus tinctorius* L.) pathosystems, respectively, others have reported altered stomatal conductance or transpiration due to disease (1,2, 11, 28). For example, Farrell et al.(11) noted increased transpiration in potato *(Solarium tuberosum* L.) due to infection by *P. infestans* (Mont.) de Bary, while Sterne et al. (28) reported decreased transpiration and stomatal conductance in avocados infected with *P. cinnamomi.* Stomatal closure is also one of the earliest responses of plants to flooding (14). We know of no work reporting transpiration and stomatal conductance of diseased plants which have been flooded.

The present studies were initiated to determine the effects of flooding, Phytophthora root rot, and their interactions on transpiration, stomatal conductance, and net CO_2 assimilation of avocado grown in Rockdale soil. Portions of this work have been published previously (25).

MATERIALS AND METHODS

Four studies (experiments 1-4) were conducted in glass greenhouses. Temperature means and ranges for experiments 1-4 were 20.8 and 9-33°C, 26.7 and 13-39°C, 24.5 and 18-30°C, and 28 and 23-33°C, respectively. Plants in all experiments were fertilized weekly with 20-20-20 plus minor elements as seedlings and alternations of 20-20-20 plus minor elements and 12-48-8 plus minor elements every 2-4 weeks after transplanting. Plants were watered about every 3-4 days.

Seedlings of 'Lula' and 'Waldin' avocado were used in experiment 1. Both of these cultivars are commonly used as rootstocks in Florida. 'Simmonds' scions grafted onto 'Waldin' rootstocks and 'Simmonds' grafted onto 'Lula' rootstocks were used in experiments 2 and 3, and experiment 4, respectively.

At the beginning of each experiment, plants were either transplanted to 15-cm-dia pots containing Promix^R potting medium (experiment 1) or to 20-cm-dia pots containing

Rockdale soil sifted through a 2.5-cm screen (experiments 2-4) amended (infested treatment) or not amended (noninfested treatment) with inoculum. Inoculum consisted of millet seed (experiments 1-3) or white sorghum seed (experiment 4) colonized by a virulent isolate of *P. cinnamomi* recovered from a declining avocado tree in Dade County; 4.2 g of inoculum was added to each 1 of mix or 0.25 g of inoculum was added to each 1 of soil in infested treatments in experiments 1 and experiments 1 and 3, respectively. Eight levels of inoculum and a noninfested control were used in experiment 4 (Fig. 2). After allowing disease to progress for 3, 6, 10, and 9 wk in experiments 1-4, respectively, infested and noninfested plants were either flooded or not flooded for 5, 14, 9, and 9 da, respectively, before an experiment was terminated.

Treatments consisted of six single plant replicates in experiment 1 and four single plant replicates in experiments 2-4 in randomized complete block designs.

Photosynthetic determinations. At the end of each experiment, transpiration, stomatal conductance, and net CO_2 assimilation were determined for all plants. These determinations were made for the fifth fully expanded leaf from the apex of each plant by enclosing the leaf in a modification of the plexiglass chamber described by Syvertsen and Smith (30). The chamber contained a fan to minimize boundary layer resistance, but the bottom was made of plexiglass instead of copper and heat exchangers were not used. Compressed air was forced through the chamber at a flow rate of 4 liters min™^{1} and relative humidity in the chamber was maintained at 50 ± 5% by mixing dry air with water-saturated air prior to entering the chamber. Light was provided by four, 500-watt, reflector, flood lamps placed above the chamber. The photosynthetic photon flux in the chamber was 900 umols s^{-1} m^{-2} as determined with a quantum sensor attached to a LI-COR 1000 data logger. A flow-through, plexiglass, water bath was positioned between the lamps and the chamber to absorb infrared radiation and maintain air temperature in the chamber at 31 ± 2°C.

Net CO_2 assimilation was determined with a Beckman model 865 infrared gas analyzer. Transpiration and stomatal conductance were determined with a General Eastern model 1100 AP dewpoint hygrometer. Calculations for all three parameters were based on those described by Jarvis (13).

Disease assays. Disease development was rated at the end of each experiment. Three different disease ratings were recorded for each plant. Disease was rated as the percentage of the total root system of a given plant which was necrotic, the percentage of 18 randomly selected, 1-cmlong, necrotic root segments from each plant from which *P. cinnamomi* was recovered, and the percent root necrosis due to the fungus (calculated by multiplying percent necrotic root tissue X percent recovery of the fungus). For recovery of *P. cinnamomi,* root segments were thoroughly washed in tap water, surface-disinfested with 95% ethanol for 30 sec, rinsed in sterile deionized water, blotted dry on sterile paper towels, placed on a selective agar medium (22), and incubated for 3 days at 25°C without light before root segments were observed for growth of *P. cinnamomi.*

RESULTS AND DISCUSSION

In general, recovery of *P. cinnamomi* from necrotic roots in these experiments was positively correlated with the percentage of a given root system which was necrotic (Fig. 1). Although all root necrosis observed in the noninfested treatments and some of the necroses observed in the infested treatments were obviously not due to *P. cinnamomi,* it is assumed that root necrosis observed in the latter treatments resulted primarily from the artificial infestation of soil with this pathogen. Since it is often difficult to recover from parasitized tissue (3, 18), *P. cinnamomi* may have been responsible for an even larger portion of the root necrosis noted in these studies than data on the recovery of the pathogen might suggest. Also, based on regression analyses, variability in the physiological parameters measured and host growth parameters were more accurately accounted for by percent root necrosis than by percent root necrosis due to *P. cinnamomi* (25; Schaff er and Ploetz, unpublished). Accordingly, percent root necrosis rather than percent root necrosis due to *P. cinnamomi* was used in Table 1 and Figs. 2-4.

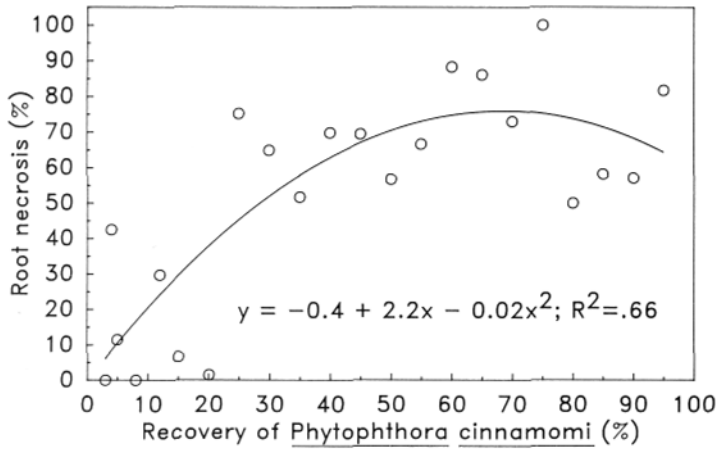

Fig. 1. Relationship between root necrosis (% of a root system which was necrotic) and recovery of *Phytophthora cinnamomi* (% root segments from which the fungus was recovered on a selective agar medium); data are from experiment 4. Root necrosis values with the same % recovery were averaged. The regression is significant ($P < 0.01$).

Phytophthora root rot and flooding interacted synergistically to reduce the health of avocado in the present studies. When compared to the noninfested, nonflooded control treatment in experiments 1-3, root rot (infested, nonflooded treatment) or flooding (noninfested, flooded) alone generally reduced the physiological parameters tested (Table 1; $P < 0.05$). However, the combined effects of root rot and flooding (infested, flooded) always significantly ($P < 0.01$) reduced these parameters; these reductions usually preceded host defoliation and death by 1-5 days (data not shown).

Table 1. Influence of Phytophthora root rot and flooding on net CO_2 assimilation (A), transpiration (E), and stomatal conductance for CO_2 (g_c) of seedling and grafted avocado.

Expt.	Host	Treat[v]	Disease[w]	Response[u] A	E	g_c
1[x]	Seedling 'Lula' and 'Waldin'	NI,NF	1.9 b	100 a	100 a	100 a
		NI,F	3.3 b	96 a	81 b	97 a
		I,NF	87.2 a	3 b	7 c	5 b
		I,F	89.9 a	3 b	9 c	6 b
2[y]	'Simmonds' scions on 'Waldin' rootstocks	NI,NF	7.5 b	100 a	100 a	100 a
		NI,F	7.5 b	48 b	39 b	35 b
		I,NF	45.0 a	90 a	95 a	90 a
		I,F	56.3 a	0 c	0 c	0 c
3[z]	'Simmonds' scions on 'Waldin' rootstocks	NI,NF	10.6 c	100 a	100 a	100 a
		NI,F	25.0 c	37 bc	66 ab	64 ab
		I,NF	53.0 b	47 b	43 bc	48 bc
		I,F	72.0 a	4 c	7 c	7 c

[u]Mean percentage of the noninfested, nonflooded control; mean separation within columns by Duncan's Multiple Range Test ($P < 0.05$).
[v]NI = noninfested; I = artificially infested with *Phytophthora cinnamomi;* NF = nonflooded; F = flooded.
[w]Mean percentage of necrotic roots.
[x]Plants grown in Promix[R] potting medium: root rot allowed to develop for 2 wk prior to flooding; data taken 5 da after flooding. Because there were no significant ($P < 0.05$) treatment by cultivar interactions, data for 'Lula' and 'Waldin' rootstocks were combined.
[y]Plants grown in Rockdale soil: root rot allowed to develop for 6 wk prior to flooding; data taken 14 da after flooding.
[z]Plants grown in Rockdale soil: root rot allowed to develop for 10 wk prior to flooding; data taken 9 da after flooding.

In experiment 2, it is not clear why the infested, nonflooded treatment did not result in the significant reductions in the physiological parameters that were noted in experiments 1, 3, and 4 (Table 1 and Figs. 3 and 4). Although percent root mortality for this treatment in experiment 2 was similar to that in experiment 3 (Table 1), significant reductions in these parameters were detected only in the latter experiment. Experiment 2 was conducted in a greenhouse without air conditioning in which temperatures reached 39°C as compared to a high of 33°C in any of the other experiments. Net CO_2 assimilation of avocado is reduced dramatically at temperatures higher than the optimal 28°C (26). It is possible that the effects of these high temperatures on transpiration, stomatal conductance, and CO_2 assimilation obscured those of root rot. Conversely, greater reductions in the physiological parameters for the flooded, noninfested treatment were presumably the result of the high temperatures in the greenhouse in which this experiment was conducted. High temperatures often accelerate damage to plants caused by flooding (23).

The dramatic reductions in the physiological parameters detected for the infested, nonflooded treatment in experiment 1 were probably the result of high root mortality due to *P. cinnamomi* in this experiment. Although initial inoculum levels of the fungus were the same in experiment 1 and for the highest inoculum level in experiment 4, symptom development was much greater in the peat-perlite potting mix (Promix) used in experiment 1 (Table 1 and Fig. 2). It is possible that the high water holding capacity of

the Promix^R potting medium may have contributed to the high levels of root rot that developed in this experiment. The development of root rot is greater in moist than in dry soil (29).

Initial levels of inoculum of *P. cinnamomi* were positively correlated with the ultimate levels of root necrosis that developed in experiment 4 (Fig. 2). In other pathosystems, increasing levels of *Phytophthora* spp. generally cause increasing levels of disease (19). In the present study, mean disease assymptopes of approximately 55 and 75% for the nonflooded and flooded treatments, respectively, were reached at relatively low inoculum levels (Fig. 2). In turn, these levels of root rot influenced the physiological parameters measured (Figs. 3, 4, and data not shown). As noted for experiments 1-3, root rot and flooding interacted strongly in experiment 4. Although the assimilation of CO_2 generally stopped in this experiment when plants with root necrosis exceeding 15% were flooded, it did not stop in nonflooded plants, even when root necrosis approached 90% (Fig. 3). Stomatal conductance appeared less sensitive than CO_2 assimilation to the interactions of root rot and flooding in this experiment; it generally decreased to 0 when root necrosis exceeded 45% in flooded plants (Fig. 4). Nonflooded plants with high levels of root necrosis in experiment 4 did not die, but did become chlorotic and partially defoliated. These symptoms are typical for Phytophthora root rot in the field (27, 33).

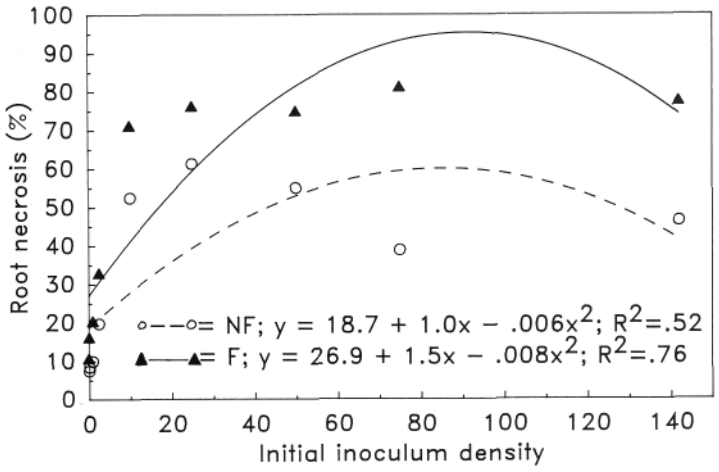

Fig. 2. Relationship between root necrosis (% of a root system which was necrotic) and initial inoculum density in experiment 4. Inoculum density = g white sorghum seed infested with *Phytophthora cinnamomi*/34 1 of soil. Each datum represents mean values for four plants; NF = nonflooded and F = flooded. Both regressions were significant ($P < 0.01$).

Although the present studies were conducted in pots in the greenhouse, we believe that the grafted plants and Rockdale soil used in most of this work adequately mimicked conditions in the field. Based on the following observations, a strong case can be made implicating Phytophthora root rot as a key factor in damage noted in Dade County avocado groves during and after tropical storm Dennis in 1981. In the present studies, foliar symptoms (chlorosis, necrosis, and defoliation) which developed on plants with

root rot which were flooded were identical to those seen in 1981 (C. W. Campbell, personal communication). Also, defoliation and mortality progressed in these plants at about the same rate as that seen after tropical storm Dennis (approximately 5-9 days after flooding). Furthermore, Phytophthora root rot is widespread in Dade County avocado groves (Ploetz, unpublished) and levels of *P. cinnamomi* used in the present studies were similar to those that are found naturally in the area (22). Although additional work needs to be conducted on the importance of root rot in nonflooded soils, this disease is obviously a serious problem in Dade County and a liability for avocado producers, considering the occurrence of hurricanes and tropical storms in the area.

Species of *Phytophthora* require high levels of moisture to produce and release zoospores (the primary infective propagule of these pathogens) (4, 10, 16, 29, 34). Therefore, the position of water tables in relation to root systems of hosts of *Phytophthora* spp. may have a great effect on disease development. In a given year, the levels of water tables in Dade County often fluctuate greatly (> 2 m) (20). Given the widespread occurrence of *P. cinnamomi* in Dade County avocado groves, it is possible that interactions between the water table and *P. cinnamomi* play an important role in determining the extent to which root rot influences avocado trees in this area.

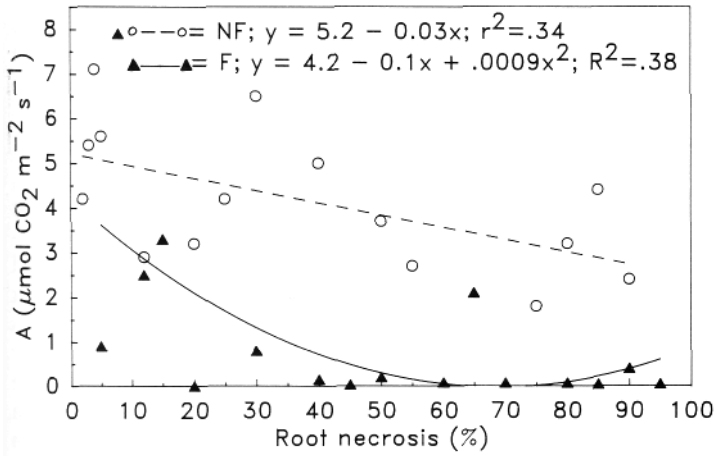

Fig. 3. Relationship between net CO_2 assimilation (A) and root necrosis (% of a root system which was necrotic) in experiment 4; NF = nonflooded and F = flooded. Assimilation values with the same % root necrosis were averaged. Both regressions were significant ($P < 0.01$).

The present work demonstrates the sensitivity of the synergism between flooding and Phytophthora root rot and how quickly it develops; after flooding, significant reductions in several physiological parameters were detected with very low levels of the fungus and root rot (Figs. 3, 4, and data not shown). These reductions occurred within 3 days of flooding (data not shown). Drew and Lynch (8) have listed possible reasons for this sort of interaction. These include increased growth or sporulation of the pathogen in flooded soil, increased infection of the host by the pathogen, decreased host response to infection, or direct effects of hypoxic and anoxic conditions on the host. Additional work is needed to elucidate the mechanisms by which Phytophthora root rot and flooding reduce the health of avocado. Such information will increase our understanding of this important disease and will benefit studies on its control.

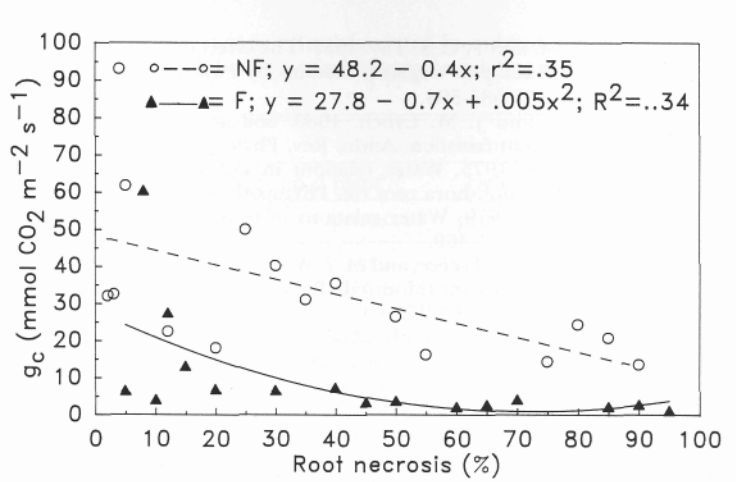

Fig. 4. Relationship of stomatal conductance for CO_2 (g_c) to root necrosis (% of a root system which was necrotic) in experiment 4; NF = nonflooded and F = flooded. Conductance values with the same % root necrosis were averaged. Both regressions were significant ($P < 0.01$).

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