

Effects of Flooding and *Phytophthora* Root Rot on Net Gas Exchange of Avocado in Dade County, Florida

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Abstract. *Phytophthora cinnamomi* Rands is widespread in avocado orchards in Dade County, Florida, but conspicuous damage caused by *Phytophthora* root rot occurs only after trees are flooded. To better understand the effects of flooding and root rot on avocado in the area, a series of greenhouse experiments was conducted in native soil that was infested or not infested with *P. cinnamomi*. Disease assessment criteria included: root necrosis, root colonization by *P. cinnamomi*, wilt defoliation, biomass accumulation, net gas exchange [net CO₂ assimilation (i.e., net photosynthesis (A), leaf conductance of CO₂ (g_c), and transpiration (E)], substomatal CO₂ concentrations (C_i), and leaf water potential (Ψ_l). In general, Ψ_l usually was not reduced unless plants were flooded for >10 days, regardless of whether or not plants were infected by *P. cinnamomi*. However, net gas exchange and biomass accumulations were usually reduced by root rot and flooding, and the combined effects of these factors on net gas exchange and biomass were usually additive. Net gas exchange declined as soon as 3 days after the onset of flooding (usually 2-3 days before plants wilted), declined soonest and most rapidly for plants with root rot, and was negatively correlated with root rot severity. Under nonflooded conditions, plants with severe root rot (up to 90% of the total root system was necrotic) were still able to assimilate CO₂, albeit at about one-half the rates of plants with low disease severities (<10% root necrosis). In contrast, after 7 days of flooding A rates were too low to detect in plants with levels of root necrosis as low as 20%. Although A and g_c were positively correlated for both flooded and nonflooded plants, A was negatively correlated with C_i, indicating that nonstomatal mechanisms may reduce A under flooded conditions. Based on results from studies with approach-grafted plants, it is apparent that factor(s) that are responsible for reduced A and g_c in flooded plants are graft-transmissible.

Most commercial avocado (*Persea americana* Mill.) production in Florida occurs in Dade County (Ruehle, 1963). Although *Phytophthora cinnamomi* Rands is widespread in avocado orchards in the area, conspicuous damage caused by *Phytophthora* root rot occurs only after trees are flooded. Although trees that are affected by root rot may wilt, defoliate, and eventually die after they are flooded (often a result of hurricanes or tropical storms), nonflooded trees with root rot usually appear healthy (Ploetz and Schaffer, 1987). Thus, the effects of *Phytophthora* root rot in Dade County often differ

from those in other production areas of the world where avocado trees may be killed or severely damaged by the disease in the absence of flooding.

We describe results from a series of greenhouse studies that were designed to address several objectives. Since *Phytophthora* root rot appeared to be a serious disease in Dade County only if trees were flooded, we sought to characterize the interactions between root rot and flooding in order to better understand the effects these factors have on avocado in Dade County. We were also interested in detecting damage caused by root rot before trees were flooded, and if reactions of non-flooded avocado trees to root rot in Dade County were similar to those of trees in production areas outside Florida. Finally, we wanted to investigate early responses of avocado to flooding and root rot. Interested readers are referred to previous publications which describe the majority of this work (Ploetz and Schaffer, 1987, 1989; Schaffer and Ploetz, 1989, 1991; Schaffer *et al.* 1991).

Materials and Methods

Experiments were conducted at the Tropical Research and Education Center of the University of Florida in Homestead. Unless otherwise specified, treatments in the experiments were 2x2 factorial combinations of flooding and infestation with *P. cinnamomi*. For convenience, the four treatment combinations were considered main effects [i.e., 1) nonflooded, noninfested; 2) nonflooded, infested; 3) flooded, noninfested; and 4) flooded, infested]. Experimental designs were randomized, complete blocks.

In general, grafted avocado plants were grown in noninfested medium (native soil or potting mix) for 1-2 mo. before being transplanted to soil infested or not infested with *P. cinnamomi* (Ploetz and Schaffer, 1987, 1989; Schaffer and Ploetz, 1989). Native soil was a Krome very gravely loam (Ruptic-Alfic Lithic Eutrochepts clayey, mixed, hyperthermic; pH ca 7.5; sand: ca 65%; silt: ca 25%, and clay: 10%).

After *Phytophthora* root rot was allowed to develop for at least 3 wks, one-half of the plants in an experiment were flooded for various lengths of time. Several different host responses were assessed before and after the imposition of flooding. Standard disease assessments that were made included root necrosis, colonization of roots by *P. cinnamomi*, wilt, defoliation, and biomass accumulations. In addition, net gas exchange, net CO₂ assimilation (i.e., net photosynthesis) (A), leaf conductance of CO₂ (g_c) and transpiration (E), internal CO₂ concentrations (C_i), and leaf water potential (Ψ) were also assessed as host responses. Techniques used for net gas exchange measurements for these experiments were described previously (Ploetz and Schaffer, 1989; Schaffer and Ploetz, 1989), and leaf water potentials were taken at shortly after solar noon with a pressure bomb (Model 3005, Soil Moisture Equipment Corp., Santa Barbara, CA 93105).

During experiments in which approach-grafted plants were used, two grafted plants ('Simmonds' scion on 'Waldin' rootstocks) were, in turn, grafted to each other about 0.3 m above the soil level in pots. Plants on one side of the graft union were subjected to

one of the four treatments described above (treated side) and plants on the other side of the union were neither flooded nor infested (nontreated side). Net gas exchange for both sides of the graft union was then assessed to determine whether the effects of flooding and root rot on avocado were graft-transmissible.

Results

Visible host responses to *Phytophthora* root rot and flooding during greenhouse experiments in native soil mimicked those observed in the field. Nonflooded plants with root rot usually could not be distinguished from those without root rot. In general, plants with root rot began to wilt about 7 day after the onset of flooding, whereas plants grown in noninfested soil either wilted 1-3 wk after infested plants or they did not wilt during a given experiment. If plants with root rot remained flooded for >10-14 days, they defoliated and eventually died.

Unless plants were flooded for >10 days, Ψ_l was generally not reduced, regardless of whether or not plants were infected by *P. cinnamomi* (data not shown). However, net gas exchange and biomass accumulations were usually reduced by *Phytophthora* root rot and flooding, and the combined effects of flooding and *Phytophthora* root rot were usually additive (Fig. 1, Table 1, and data not shown). Net gas exchange declined as soon as 3 days after the onset of flooding, declined soonest and most rapidly for plants with *Phytophthora* root rot, and was negatively correlated with root rot severity (Figs. 1 and 2A, and data not shown). Under nonflooded conditions, plants which had high levels of root necrosis (up to 90%) were still able to assimilate CO₂, although at rates 50% lower than plants which had relatively low root rot severities (<10%). In contrast, A rates of flooded plants with as low as 20% root necrosis were nondetectable after 7 days of flooding (Fig. 2A and data not shown).

Net CO₂ assimilation and g_c were positively correlated in several different experiments and the curvilinear association shown in Fig. 2B is typical of results from other experiments; the relationship between A and g_c was the same for flooded and nonflooded plants. The relationship between A and C_i was also similar for flooded and nonflooded plants (although y-intercepts for the flooded and nonflooded regressions in Fig. 2C differed, their slopes did not). During studies with approach-grafted plants, flooding, root rot, and the combination of these factors usually reduce A, g_c , and E in plants on both the treated and nontreated side of the graft union (Fig. 3 and data not shown).

Discussion

This work corroborates previous studies which indicated that the effects of *Phytophthora* root rot on avocado were greatest when plants were flooded (Wager, 1942; Zentmyer and Klotz, 1947). The effects of flooding and root rot on avocado were usually additive during our work (Fig. 1, Table 1 and data not shown). We also determined that changes in net gas exchange are sensitive and early host responses to both flooding and root rot and that root rot often reduced net gas exchange in the absence of flooding. During our

work, the magnitude and statistical significance of these reductions depended upon root rot severity and possibly other factors such as ambient temperature and light intensity (Fig 2A and data not shown). Ayres (1980) noted that although reductions in net gas exchange are usually inconsequential for diseases that cause rapid tissue death, they are very important for diseases which have a less dramatic effect on the host. Thus *Phytophthora* root rot may exert a significant effect on avocado in Dade County, even in the absence of flooding.

Sterne *et al.* (1978) indicated that g_c and E of avocado (cv. Bacon) in California was reduced by root rot and that afternoon Ψ_l in these plants was also reduced. They proposed that stomatal function of trees with root rot was adversely affected by changes that occurred in the water transport systems of such plants, and that reduced water status of affected plants was probably the primary factor involved in root rot symptom development (i.e. wilt and dieback) and reduced productivity caused by this disease. Although we did not observe the reductions in Ψ_l that were reported by Sterne *et al.* (1978), we did corroborate their observations that root rot reduced g_c and E of avocado.

The negative correlation between A and C_i suggested that CO_2 concentrations on leaves of flooded and nonflooded plants did not limit photosynthetic rates during our work. Consequently, nonstomatal mechanisms may reduce A of avocado under flooded conditions. Based on results from studies with approach-grafted plants, it is apparent that factor(s) that are responsible for reduced A and g_c in flooded plants are graft-transmissible (Fig. 3).

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Table 1. Effect of *Phytophthora* root rot and flooding on the growth of grafted avocado plants ^x

Experiment ^y	Treatment ^z	Root Necrosis (%)	Dry weight (g)		
			Root	Shoot	Plant
1	-P, -F	4.5c	19.3c	32.6a	51.9a
	-P, +F	12.2c	8.5b	28.2ab	36.8b
	+P, -F	37.5b	18.6a	26.0b	44.6ab
	+P, +F	62.5a	7.7b	17.0c	24.7c
2	-P, -F	10.6c	19.4a	45.4a	64.8a
	-P, +F	20.0c	11.8b	35.3ab	47.1ab
	+P, -F	53.0b	11.4b	25.9ab	37.2b
	+P, +F	72.0a	9.0b	22.8b	31.7b

^x Grafted plants were 'Simmonds' scions on Waldin rootstocks. For an experiment, mean values within a column are not significantly different from each other if followed by the same letter according to Duncan's multiple range test ($P \leq 0.05$).

^y In experiments 1 and 2, *Phytophthora* root rot was allowed to develop for 6 and 10 wks and plants were flooded for 28 and 9 days, respectively.

^z -P and + P = noninfested and infested with *P. cinnamomi* and -F and + F = nonflooded and flooded.

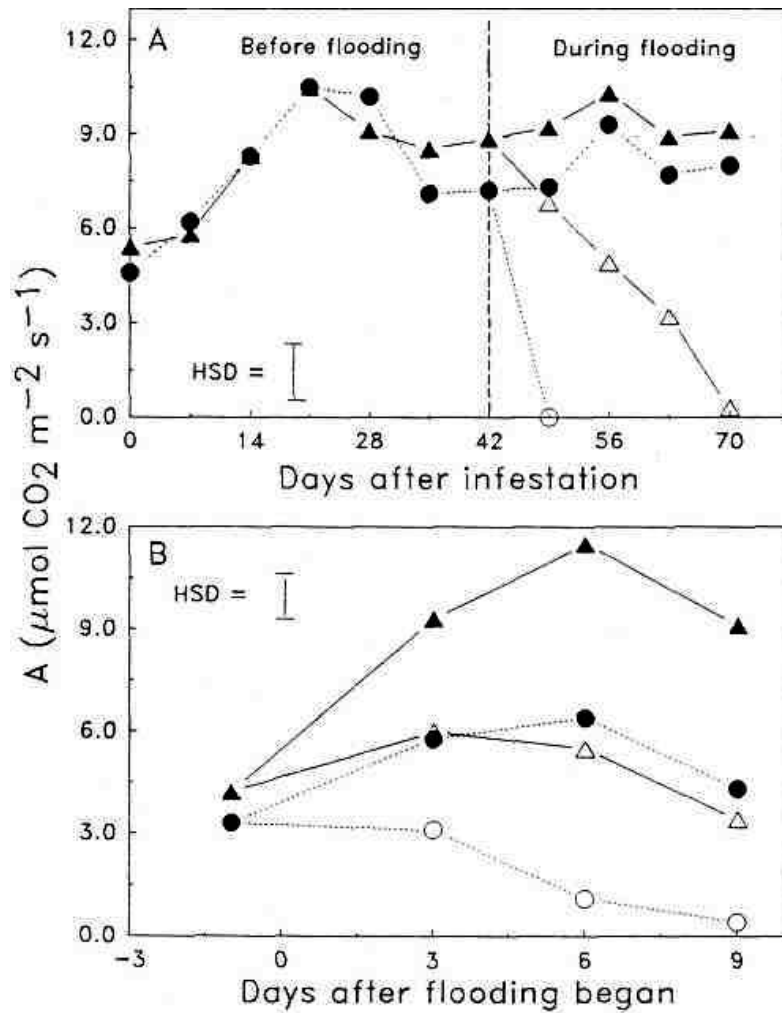


Fig. 1. A) Net CO₂ assimilation (A) of grafted avocado plants ('Simmonds' scions on Waldin rootstocks) growing in Krome very gravely loam. Infested with *P. cinnamomi* = ●, ○; noninfested = △, ▲; flooded = ○, △; nonflooded = ●, ▲. Each datum represents the mean response of four plants. HSD = pooled honestly significant difference according to Tukeys studentized range test (P<0.05). B) Net CO₂ assimilation (A) for plants from a repeat of the experiment in Fig. 1A in which net gas exchange was monitored on a more frequent basis.

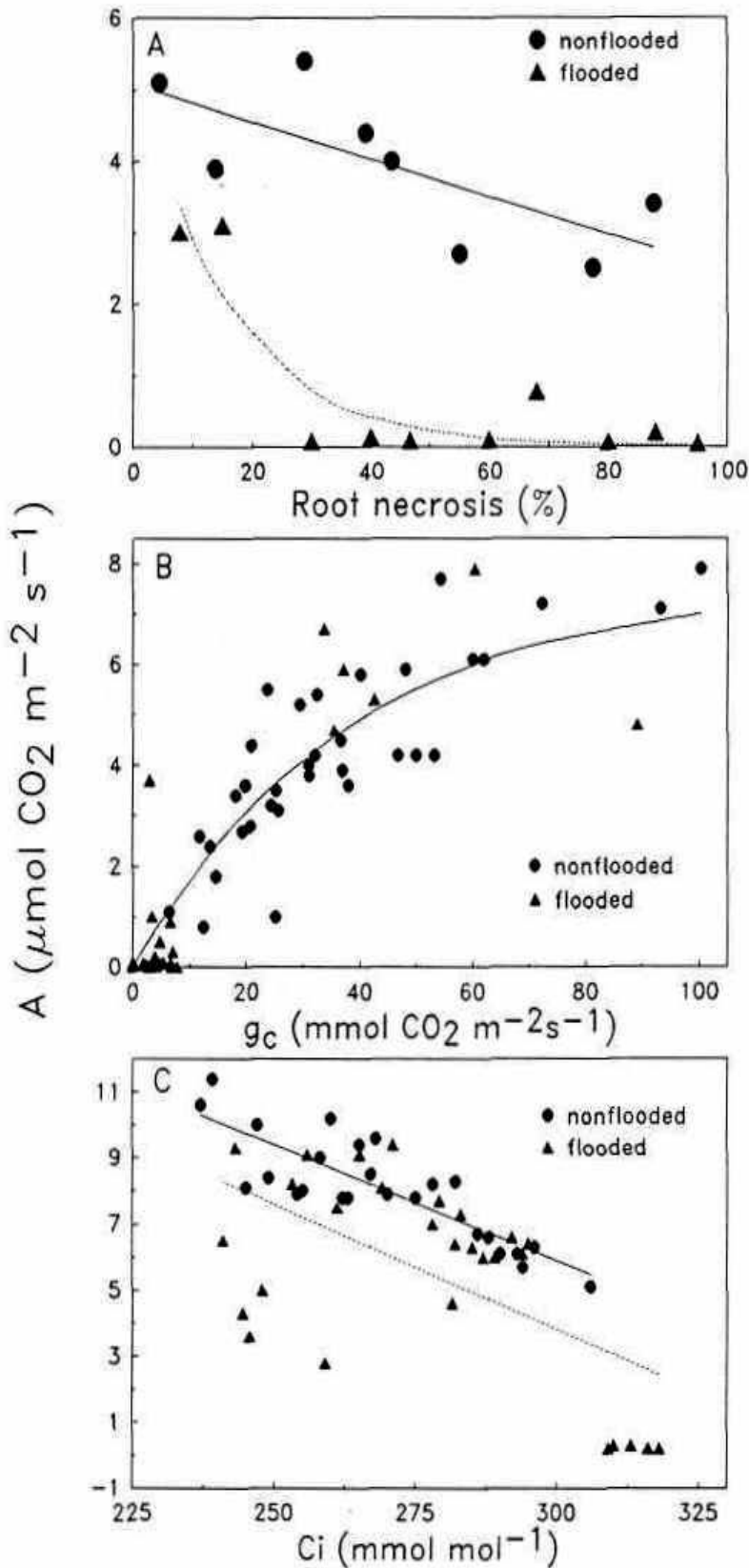


Fig. 2. A). Net CO₂ assimilation (A) and percent root necrosis for flooded (\blacktriangle — \blacktriangle) and nonflooded (\bullet — \bullet), grafted avocado plants ('Simmonds' scions on Lula rootstocks). Each datum represents mean A for a given level of root necrosis. Soil was artificially infested with different levels of *P. cinnamomi* to achieve a range of root rot severities; a total of 36 flooded and 36 nonflooded plants were tested. Regression lines for flooded and nonflooded plants are $y = 5.6e^{-0.65x}$ ($R^2 = 0.83$) and $y = 5.1^{-0.26x}$ ($r^2 = 0.53$), respectively. Both regressions are significant ($P \leq 0.01$). B) Net CO₂ assimilation (A) and stomatal conductance of CO₂ (g_c) for flooded and nonflooded, grafted avocado plants in Fig. 2A; each datum represents a single plant. The regression line for flooded and nonflooded plants combined is $y = 7.57(1 - e^{-0.26x})$ ($R^2 = 0.85$). The regression is significant ($P \leq 0.01$). C) Net CO₂ assimilation (A) and substomatal CO₂ concentration (C_i) for flooded and nonflooded avocado plants in Fig. 2A. The regression lines for flooded and nonflooded plants are $y = 9.45 - 0.071x$ and $y = 11.2 - 0.69x$, respectively. The y-intercepts, but not the slopes of the regression lines are different ($P \leq 0.05$).

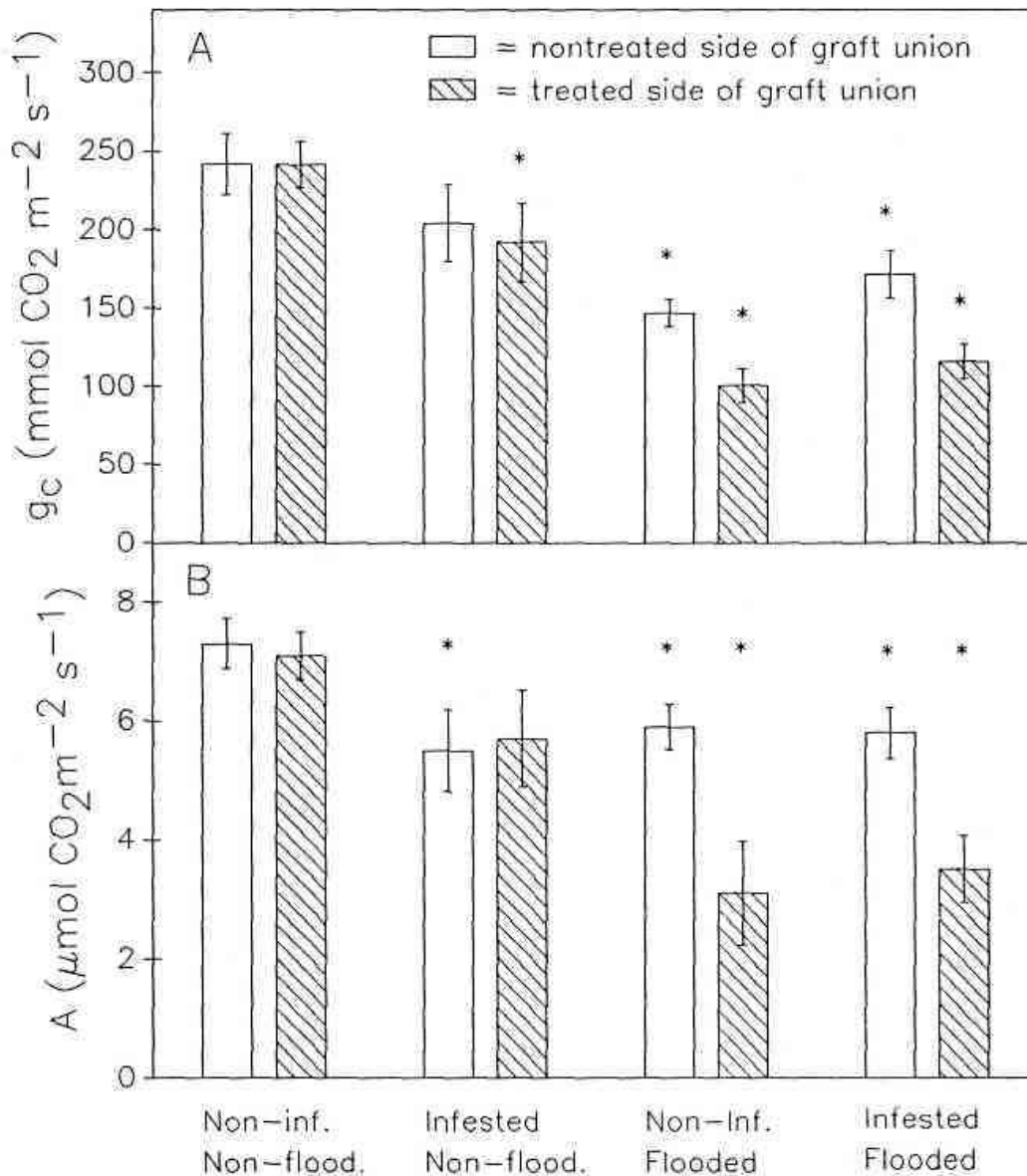


Fig. 3. **A**) Stomatal conductance of CO_2 (g_c), and **B**) net CO_2 assimilation (A) for pairs of approach-grafted avocado plants. Approach-grafted plants were 'Simmonds' scions grafted on Waldin rootstocks. Plants on one side of the graft union were subjected to one of four treatments listed beneath the x-axis (treated side of union) and plants on the other side of the union were not flooded or infested (nontreated side). Bars are standard errors of means for four plants and * denotes significant differences from the noninfested, nonflooded check means based on t-tests ($P \leq 0.05$).