

Effects of Flooding and Phytophthora Root Rot on Net Gas Exchange and Growth of Avocado

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ABSTRACT

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Greenhouse studies were conducted to determine the effects of Phytophthora root rot (caused by *Phytophthora cinnamomi*) and flooding on avocado (*Persea americana*). In addition to standard disease assessments (root necrosis, root colonization, wilt, and defoliation), dry weight accumulations and gas exchange characteristics were monitored as indicators of host distress. In a peat-perlite potting medium with a high water-holding capacity, net CO₂ assimilation, transpiration, stomatal conductance for CO₂, and root and shoot dry weights were reduced by root rot ($P < 0.05$). In this medium, flooding alone generally did not reduce these parameters after 5 days. In a calcareous soil used for avocado production in south Florida (with a lower water-holding capacity than the potting medium), root rot reduced assimilation, transpiration, and conductance in a series of three experiments, although not consistently. In

this soil, flooding alone reduced these parameters as well. After 4 wk of flooding, assimilation, transpiration, and conductance declined to nondetectable levels. However, when plants with root rot were flooded, these physiological parameters were reduced as soon as 3 days after flooding began, and they declined to nondetectable levels within 1 wk. These plants also had reduced root, shoot, and total plant dry weight accumulations and increased defoliation when compared with nonflooded plants without root rot. Although similar reductions occurred for nonflooded plants with root rot and flooded plants without root rot, these reductions were not as great or consistent as those detected for the combined root rot and flooding treatment. In combination, Phytophthora root rot and flooding dramatically impaired photosynthesis and normal stomatal function and reduced the root and shoot biomass in avocado.

Additional keywords: avocado root rot, net photosynthesis.

Phytophthora root rot, caused by *Phytophthora cinnamomi* Rands, is the primary constraint to avocado (*Persea americana* Mill.) production in most areas in which this fruit is produced (5-7,25,31,38,42,43). Although the prevalence and severity of root rot in the Caribbean basin has resulted in widespread losses, this disease is conspicuous in certain areas of the region (e.g., Florida) only during periods of flooding (28); hurricanes and tropical storms in the Caribbean are responsible periodically for heavy rains.

Flood tolerance varies widely among plant species (18). Although some plants are able to adapt to continuous flooding, others are unable to withstand submersion for more than 1 or 2 days (15). Water-logged soils influence the impact of many diseases (10), perhaps most notably those caused by species of *Phytophthora*. Saturated or flooded conditions are associated with increases in severity of root rots of alfalfa, caused by *P. megasperma* f. sp. *medicaginis*; walnut caused by *P. cinnamomi*, *P. citricola*, *P. citrophthora*, and *P. cryptogea*; tomato, caused by *P. parasitica*, *P. capsici*, and *P. cryptogea*; jarrah, caused by *P. cinnamomi*; and avocado, caused by *P. cinnamomi* (4,9,19,21,28). It is not clear whether, under conditions of high soil moisture, the severity of these diseases increases as a result of altered soil chemistry, reduced host resistance, enhanced activities of these pathogens, or a combination of these factors (10).

An early response of plants to flooding (8,17,23,26) and disease (2,3,11,34) is stomatal closure. Consequently, researchers have used stomatal function and associated host characteristics (e.g., net assimilation of CO₂, transpiration, and stomatal conductance) when monitoring host response in flooding or disease studies. Ayres (2) noted that although reductions in these parameters are inconsequential for diseases that result in widespread and rapid death of tissue, they are very important for diseases having a less dramatic effect on the host (e.g., Phytophthora root rot of avocado in Florida). Growth and survival of plants in the latter category often are adversely, but inconspicuously, affected.

Because the effects of Phytophthora root rot on avocado often

are inconspicuous in the absence of flooding in Florida, we became interested in determining the influence of this disease under flooded and nonflooded conditions. We chose several ways of assessing host response. We determined the effects of root rot and flooding on net CO₂ assimilation, transpiration, and stomatal conductance for CO₂ of avocado. Although numerous reports have been published on the effects of disease (2,3) or flooding (8,23,26) on stomatal function and photosynthesis, we know of no published work describing the interaction of disease and flooding on these host parameters. We also monitored the effects of root rot and flooding on root, shoot, and total plant dry matter accumulations and root:shoot ratios. Dry matter accumulations and root:shoot ratios have been used previously to monitor host response during studies on the effects of disease (1,22,24,41) and flooding (33,37) on host growth. In addition, we used standard disease assessments (disease severity and root colonization by *P. cinnamomi*) not made during previous studies on root rot and flooding (39,45). Portions of this work have been reported previously (28,29).

MATERIAL 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, 28 and 23-33 C, 26.7 and 13-39 C, and 24.5 and 18-30 C, respectively. Plants in all experiments were fertilized weekly with 20-20-20 plus minor elements as seedlings, and with alternations of 20-20-20 plus minor elements and 12-48-8 plus minor elements every 2-4 wk after transplanting. Plants were watered about every 2-4 days. Also, the level of water in reservoirs containing flooded plants was maintained constant by adding water when necessary.

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

At the beginning of each experiment, plants were either transplanted to 15-cm-diameter pots containing a peat-perlite (Promix, Premier Brand Inc., New Rochelle, NY) potting medium

(experiment 1) or to 20-cm-diameter pots containing Rockdale fine sandy loam that had been sifted through a 2.5-cm screen (experiments 2-4). This soil is a native, calcareous soil in which most avocados in south Florida are grown. Based on soil dilution assays conducted with a selective medium containing, among other ingredients, cornmeal agar, hymexazol (Sankyo Co., Shiga-Ken, Japan), and pimarinin (Gist-brocades, Charlotte, NC) (27), the Rockdale soil used in these experiments was determined to be free of *P. cinnamomi*. Potting medium and soil were either amended (infested treatment) or not amended (noninfested treatment) with inoculum. Inoculum consisted of sorghum seed (experiment 2) or millet seed (experiments 1, 3, and 4) on which a virulent isolate of *P. cinnamomi*, which had been recovered from a declining avocado tree in Dade County, FL, had been grown for about 4 wk. Each liter of medium in experiment 1 was infested with 4.2 g of inoculum, and 0.25 g of inoculum was added to each liter of soil used in experiments 3 and 4. In experiment 2, both levels of inoculum were tested. These rates convert to 420, 8 and 120, 25, and 25 infested seed added to each liter of potting mix or soil in experiments 1-4, respectively. After allowing disease to progress for 3, 9, 6, and 10 wk in experiments 1-4, respectively, plants in infested and noninfested pots either were flooded or not flooded for additional periods of 5, 9, 28, and 9 days, respectively. Flooded pots were placed in fiberglass reservoirs filled with tap water such that the surface of the soil was about 1 cm below the surface of the water.

Treatments consisted of six single-plant replicates per cultivar in experiment 1 and four single-plant replicates in experiments 2-4 in randomized complete block designs. Plants were blocked on the basis of size before transplanting in infested or noninfested soil at the beginning of an experiment.

Disease and plant growth assays. Two parameters were used to evaluate disease severity at the end of each experiment. The percentage of the total root system of a given plant that was necrotic was estimated visually, and, for each plant, the percentage of 18 randomly selected, 1-cm-long, necrotic root segments from which *P. cinnamomi* was recovered were each used as disease ratings. For recovery of *P. cinnamomi*, root segments were washed thoroughly in tap water, surface-disinfested with 95% ethanol for 30 sec, rinsed in sterile deionized water, blotted dry on sterile paper towels, placed on the selective medium, and incubated for 3 days at 25 C without light before root segments were observed for growth of *P. cinnamomi*.

At the end of each experiment, plant height and root and shoot dry weights were determined. Plant tissue was dried at 70 C for 4 days for dry weight determinations. Viable root:shoot ratios (VRSR) were calculated with the formula:

$$\text{VRSR} = [\text{RT} - (\text{RT} \times \text{RN})] / \text{ST},$$

where RT is root dry weight, RN is root necrosis as the proportion of the total root system that was necrotic, and ST is shoot dry weight. In experiments 2 and 4, defoliation was calculated as the number of nodes without leaves divided by the total number of nodes. In experiment 3, a subjective 1-5 scale (1 indicates no wilt and 5 indicates extreme wilt) was used to rate wilt symptom development at the end of the experiment.

Gas exchange determinations. Gas exchange determinations were made in the laboratory; plants were moved from the greenhouse on the morning of each determination. Net assimilation of CO₂, transpiration, and stomatal conductance for CO₂ were determined periodically by using the fifth fully expanded leaf from the apex of each plant; the same leaf was used throughout a given experiment. During these determinations, each leaf was enclosed in a modification of the Plexiglas chamber described by Syvertsen and Smith (36). Compressed air was forced through the chamber at a flow rate of 4 L min⁻¹; relative humidity in the chamber was maintained at 50 ± 5% by mixing ambient air with water-saturated air before it entered the chamber. Light was provided by four 500-W, reflector flood lamps placed above the chamber. The photosynthetic photon flux in the chamber was 900 μmol sec⁻¹ m⁻², as determined with a quantum sensor attached to a Li-Cor 1000

data logger (Li-Cor, Inc., Lincoln, NE); the light saturation point for avocado is reported to be 500 μmol sec⁻¹ m⁻² (30). A flow-through, Plexiglas 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. Optimal temperatures for photosynthesis of avocado range from 25 to 33 C (30).

Net assimilation of CO₂ was determined with a Beckman model 865 infrared gas analyzer (Beckman Instruments, Inc., Fullerton, CA). Transpiration was determined with a General Eastern model 1100 AP dewpoint hygrometer (General Eastern Instruments Corp., Watertown, MA), and stomatal conductance was calculated from transpiration. Calculations for all three parameters were based on those described by Jarvis (16). Leaf area in the chamber was determined with an Li-Cor 3000 leaf area meter (Li-Cor, Inc. Lincoln, NE).

Statistical analyses. The treatment combination in these experiments was a 2 × 2 factorial. Therefore, an analysis of variance was performed to test for significant interactions between Phytophthora root rot and flooding with respect to disease ratings, plant growth parameters, and photosynthetic characteristics. However, we were primarily interested in the treatment or treatment combination (Phytophthora root rot, flooding, and root rot and flooding) that had the greatest effect on these parameters. Thus, additional analyses were performed that considered the main effects (root rot and flooding) and the combination of the two as individual treatments.

RESULTS

Experiment 1 (potting medium). No significant interactions were detected between cultivar and treatment ($P < 0.05$) for any parameter measured. Therefore, both cultivars were combined for statistical analyses. Also, there were no significant interactions between infested (root rot) and flooding treatments ($P < 0.05$) (Table 1). Root necrosis was greater for plants in the infested than the noninfested treatments (Table 2). Flooding, however, did not cause any significant increase in root necrosis (Tables 1 and 2). *P. cinnamomi* was recovered from more than 90% of the necrotic roots from plants grown in infested potting medium but was never recovered from plants grown in noninfested medium (data not shown).

At the end of experiment 1, inoculated plants had reduced root, shoot, and total plant dry weights compared with uninoculated plants (Table 2). Also, the viable root:shoot ratio was lower for plants with root rot (Tables 1 and 2). Flooding had no effect on plant growth in this experiment (Tables 1 and 2).

Net CO₂ assimilation was reduced as soon as 7 days after plants were transplanted into infested soil. In contrast, assimilation increased slightly over time for plants in noninfested soil. By 14

TABLE 1. Effects of Phytophthora root rot (P) and flooding (F) on the growth of avocado: Test for main effects and interactions^a

Experiment	Treatment	Root necrosis (%)	Dry weight			Viable root:shoot ratio
			Root	Shoot	Plant	
1 (potting medium)	P	*	*	*	*	*
	F	NS	NS	NS	NS	NS
	P×F	NS	NS	NS	NS	NS
2 (Rockdale soil)	P	*	*	*	*	*
	F	*	NS	NS	NS	*
	P×F	NS	NS	NS	NS	NS
3 (Rockdale soil)	P	*	NS	*	*	*
	F	*	*	*	*	*
	P×F	*	NS	NS	NS	NS
4 (Rockdale soil)	P	*	*	*	*	*
	F	*	*	NS	NS	*
	P×F	NS	NS	NS	NS	NS

^a* = significantly different from the noninfested, nonflooded control or a significant interaction (P×F) according to a studentized *t*-test at $P < 0.05$; NS = nonsignificant at $P < 0.05$.

days after transplanting, assimilation was 75% lower for plants in infested soil than for plants in noninfested soil (Fig. 1). Flooding alone had no effect on assimilation, whereas the combination of flooding and pathogen resulted in reductions in assimilation no greater than those detected for inoculated plants (Fig. 1).

The effects of flooding on transpiration and stomatal conductance were almost identical to that on assimilation (data not shown). Thus, there was a strong linear correlation between assimilation and conductance (Fig. 2; $r^2 = 0.92$). In general, plants without root rot were grouped at the top of the regression line and plants with root rot were grouped at the bottom of the line.

Experiments 2-4 (Rockdale soil). For root necrosis data,

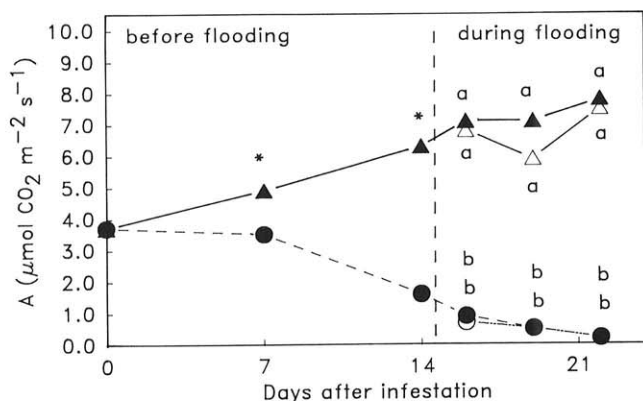


Fig. 1. Effect of *Phytophthora* root rot and flooding on net CO_2 assimilation (A) of avocado seedlings growing in a peat-perlite potting medium. Infested with *P. cinnamomi* = \circ, \bullet ; noninfested = Δ, \blacktriangle ; flooded = \circ, Δ ; nonflooded = \bullet, \blacktriangle . For mean assimilation values for a given time after infestation, asterisks indicate significance according to studentized *t*-test ($P < 0.05$); different letters indicate significance according to Tukey's studentized range test ($P < 0.05$).

significant interaction was found between *Phytophthora* root rot and flooding only in experiment 3 (Table 1). Root necrosis always was greater for infested than for noninfested treatments (Table 2). In experiment 2, root necrosis for the high and low inoculum levels was not significantly different. Also, root necrosis was greater for flooded treatments than for the nonflooded control, and the combination of root rot and flooding always resulted in the greatest root necrosis (Table 2). *P. cinnamomi* was recovered frequently from necrotic roots of plants in infested soil, but it was never recovered from necrotic roots of plants in noninfested soil.

In Rockdale soil, there were no significant interactions between root rot and flooding with respect to root, shoot, and total plant dry weight, nor for viable root:shoot ratio (Table 1). Under nonflooded conditions, root rot caused a significant reduction in

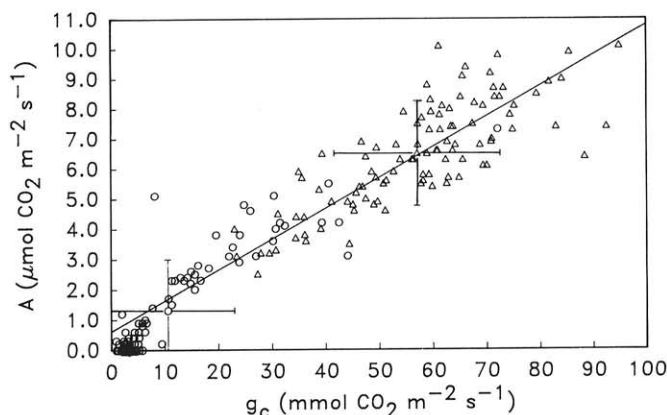


Fig. 2. Net CO_2 assimilation (A) vs. stomatal conductance (g_c) for potted avocado seedlings growing in a peat-perlite potting medium. Infested with *P. cinnamomi* = \circ ; noninfested = Δ . At mean A and g_c values for infested and noninfested treatments, error bars represent 1 SE for x and y axes.

TABLE 2. Effect of *Phytophthora* root rot and flooding on the growth of seedling and grafted avocado

Experiment ^u	Treatment ^v	Root ^w necrosis (%)	Dry weight (g)			Viable root:shoot ratio ^x
			Root	Shoot	Plant (root + shoot)	
1	-P,-F	1.9b ^y	3.7a	9.3a	13.0a	0.40a
	-P,+F	3.2b	2.5ab	8.2ab	10.7ab	0.29a
	+P,-F	89.1a	1.9b	6.4b	8.3b	0.03b
	+P,+F	86.3a	1.9b	6.8b	8.7b	0.03b
2	-P,-F	7.5c,b ^z	24.6a,a	49.9ab,ab	74.5ab,ab	0.46a,a
	-P,+F	10.8c,b	24.3a,a	63.2a,a	87.6a,a	0.33b,ab
	(high) +P,-F	46.3b	15.3ab	35.2b	50.5b	0.24b
	(high) +P,+F	77.5a	12.5b	31.0b	43.6b	0.09c
	(low) +P,-F	52.5 a	18.0 a	41.7 b	59.7 ab	0.21 bc
	(low) +P,+F	71.3 a	18.0 a	37.5 b	55.5 b	0.12 c
3	-P,-F	4.5c	19.3a	32.6a	51.9a	0.56a
	-P,+F	12.2c	8.5b	28.2ab	36.8ab	0.27c
	+P,-F	37.5b	18.6a	26.0b	44.6b	0.45b
	+P,+F	62.5a	7.7b	17.0c	24.7c	0.17d
4	-P,-F	10.6c	19.4a	45.4a	64.8a	0.39a
	-P,+F	20.0c	11.8b	35.3ab	47.1ab	0.33ab
	+P,-F	53.0b	11.4b	25.9ab	37.2b	0.20ab
	+P,+F	72.0a	9.0b	22.8b	31.7b	0.17b

^u Experiment 1 utilized Lula and Waldin seedlings in a peat + perlite potting medium; data are means for both cultivars. Experiments 2-4 utilized grafted plants in Rockdale soil: Simmonds scions on Lula rootstocks and Simmonds scions and Waldin rootstocks were used in experiment 2, and experiments 3 and 4, respectively.

^v -P and +P = noninfested and infested with *P. cinnamomi*, and -F and +F = nonflooded and flooded, respectively. Levels of infestation varied with experiment: experiment 1 = 4.2 g inoculum per liter of mix; experiment 2 = 4.2 g (high) and 0.25 g (low)/L of soil; experiments 3 and 4 = 0.25 g/L of soil.

^w Percent root necrosis was estimated visually for each root system at the end of an experiment.

^x Viable root:shoot ratio = $[RT - (RT \times RN)]/ST$, where RT = root dry weight, RN = proportion of a root system that was necrotic, and ST = shoot dry weight.

^y Means within a column for a given experiment followed by the same letter are not significantly different according to Duncan's multiple range test at $P < 0.05$.

^z Two mean separations were computed for experiment 2; letters following means for the high infested treatments are compared with the first letter(s) following means for the noninfested treatments (-P,-F and -P,+F) and letter(s) following means for the low infested treatments are compared with the second letter(s) following means for the noninfested treatments.

root dry weight only in experiment 4 (Table 2). However, shoot dry weight was reduced by this disease in all three experiments conducted in Rockdale soil (Table 2); total plant dry weight was reduced in experiments 2 and 3. Root rot always reduced viable root:shoot ratios (Table 2). Flooding alone significantly reduced root dry weight in experiments 3 and 4, but shoot and plant dry weights were not significantly reduced by flooding in any of the experiments (Table 2). The viable root:shoot ratio always was reduced by flooding (Table 2). The combination of root rot and flooding always resulted in the lowest root, shoot, and total plant dry weights, as well as the lowest viable root:shoot ratios in these experiments (Table 2). The combination of root rot and flooding also increased defoliation and wilt ($P < 0.05$) in experiments where these parameters were measured (2 and 4, and 3, respectively); individually, root rot and flooding did not increase defoliation and wilt (data not shown).

Net CO_2 assimilation declined rapidly after the onset of flooding for plants that had *Phytophthora* root rot (Figs. 3 and 4 and data not shown). In general, transpiration and stomatal conductance had trends similar to those for assimilation (data not shown). Assimilation was reduced within 3 days of flooding for infested plants in experiment 4 (Fig. 3) and declined to nondetectable levels after 9, 9, and 7 days in experiments 2–4, respectively (data not shown and Figs. 3 and 4). Also, reductions in assimilation occurred before the development of aboveground symptoms usually associated with advanced stages of root rot (e.g., wilt and defoliation).

The individual effects of root rot and flooding on assimilation were less clear. At the end of experiment 4, there was a significant decrease in assimilation due to root rot in the absence of flooding (Fig. 4). No reductions in assimilation due to root rot alone were detected in experiments 2 and 3 (data not shown and Fig. 4). Flooding alone caused a significant decrease in assimilation in experiment 3 after 14 days (Fig. 3).

DISCUSSION

Our work corroborates results from previous studies on the interaction of *Phytophthora* root rot and flooding, which demonstrated the sensitivity of avocado to flooding when it is infected by *P. cinnamomi* (39,45). Our work differs from these studies (39,45), however, by rating disease severity. In the present study, root rot severities in experiments that used Rockdale soil (experiments 2–4) were greatest when plants were flooded (Table 2). Because uniform levels of inoculum were used to infest flooded and nonflooded treatments in these experiments, we assume the increased root necrosis detected for plants in the flooded, infested treatment was due to flooding. Flooding may have increased production and dissemination of zoospores of *P. cinnamomi* (12,35,44) or resulted in other deleterious interactions, as suggested

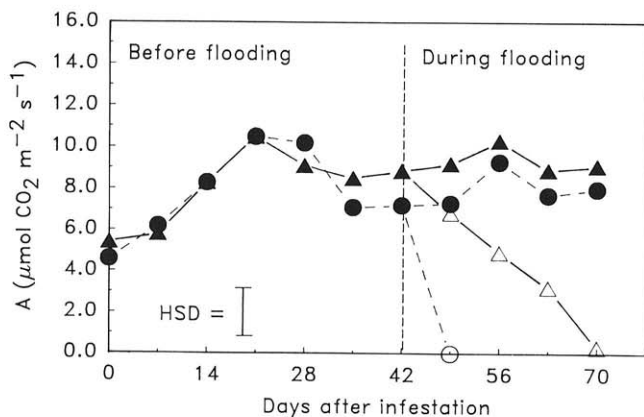


Fig. 3. Net CO_2 assimilation (A) of grafted avocado plants growing in Rockdale soil (experiment 3). Infested with *P. cinnamomi* = \circ , \bullet ; noninfested = Δ , \blacktriangle ; flooded = \circ , Δ ; nonflooded = \bullet , \blacktriangle . HSD = pooled honestly significant difference according to Tukey's studentized range test ($P < 0.05$).

by Drew and Lynch (10). Although the effects of root rot severities in nonflooded soil comparable to those that developed in flooded soil were not tested (severities were always 20–25% greater in flooded soil), preliminary evidence from other work suggests that, in the absence of flooding, avocados do not die in Rockdale soil when levels of root rot range as high as 90% (28). In addition, mortality does occur under flooded conditions when levels of root rot are substantially lower than those studied in the present work (approximately 15–40%). Obviously, flooding and *Phytophthora* root rot coact in Rockdale soil to dramatically reduce the health of avocado.

In contrast to results from experiments conducted with Rockdale soil, root necrosis was not greater in flooded than in nonflooded, infested potting medium in experiment 1 (Table 2). Presumably, this was due to the high water-holding capacity of this medium (>600%). Because the potting medium remained saturated during experiment 1, high soil-water status during this experiment may have caused the high level of root rot detected for plants in the infested, nonflooded treatment.

Host photosynthesis, transpiration, and stomatal conductance were greatly inhibited in root-rotted plants that were flooded during experiments conducted in Rockdale soil (experiments 2–4). Reductions in assimilation, transpiration, and conductance were detected within 3 days of flooding in experiment 4, and probably occurred before then, based on early development of symptoms (wilt and defoliation) in some of these plants.

In previous work with potted avocados infected with *P. cinnamomi*, no obvious effect of root rot in nonflooded soil was observed (39,45). By monitoring photosynthetic characteristics of potted plants, we found that avocado is affected by root rot in the absence of flooding, even though these plants often show no foliar symptoms of this disease. Reductions in assimilation, transpiration, and stomatal conductance for nonflooded plants with root rot were significant ($P < 0.05$) in experiments 1 and 4 but were not significant in experiments 2 and 3. Although other work by us (28) suggested that levels of root rot higher than those used in experiments 2–4 may be necessary for significant reductions in assimilation, transpiration, and conductance to be detected in Rockdale soil in the absence of flooding, additional work is needed to determine what levels of root rot result consistently in these reductions.

Plant biomass accumulations often were reduced by root rot, whether or not these plants were flooded; reductions were greatest, however, for root-rotted plants that were flooded (Table 2). Although the reductions in biomass detected for plants with root rot probably resulted, in part, from impaired photosynthesis in these plants, it is also probable that portions of these reductions resulted from direct or other indirect effects of root rot on the host (34,40). The reduced shoot weight and root:shoot ratios detected above suggest a need to monitor the partitioning of host

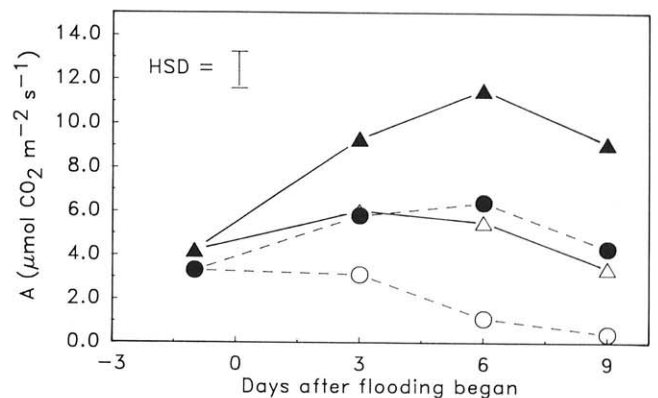


Fig. 4. Net CO_2 assimilation (A) of grafted avocado plants growing in Rockdale soil (experiment 4). Infested with *P. cinnamomi* = \circ , \bullet ; noninfested = Δ , \blacktriangle ; flooded = \circ , Δ ; nonflooded = \bullet , \blacktriangle . HSD = pooled honestly significant difference according to Tukey's studentized range test ($P < 0.05$).

photosynthates during this work. Schulze (32) indicated that an increased amount of fixed carbon is allocated to root growth when a plant's root:shoot ratio is reduced.

In experiments 2-4, reductions in assimilation, transpiration, and stomatal conductance for root-rotted plants that were flooded preceded the appearance of wilt and defoliation by as much as 3 days (data not shown). Others (13,20) have reported reduced assimilation and/or stomatal conductance for plants affected by wilt-type diseases in advance of wilt symptoms. For these diseases and *Phytophthora* root rot of avocado, reduced host photosynthesis and stomatal conductance are earlier indicators of host distress than are the conspicuous foliar symptoms usually associated with these diseases.

Avocado responds to root rot and flooding by closing its stomata (present study); as a result of reduced evapotranspiration, plant turgor is maintained. Although it is possible that reduced stomatal conductance may cause reductions in net assimilation of CO₂ of avocado, it is not clear whether reduced assimilation was the effect or cause of reduced conductance in our work. Often, if assimilation is reduced, the increased internal CO₂ concentration in the leaf mesophyll results in decreased conductance (14). Additional work is needed to clarify this sequence of events and to identify mechanisms by which *Phytophthora* root rot and flooding reduce CO₂ assimilation and stomatal conductance in avocado.

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