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Net Gas Exchange as a Damage Indicator for Phytophthora Root Rot of Flooded and Nonflooded Avocado

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Abstract. **Net CO_2 assimilation (A) and stomatal conductance for CO_2 (g_s) were determined for flooded and nonflooded avocado plants *(Persea americana Mill.)* with different severities of phytophthora root rot (caused by *Phytophthora cinnamomi* Rands). Under nonflooded conditions, root necrosis (primarily due to *P. cinnamomi*) of <50% generally had little effect on net gas exchange, whereas root necrosis ≥50% resulted in decreases in A and g_s of up to 65% when compared to noninfested controls. However, root necrosis ≥20% greatly reduced A and g_s when plants were flooded for 7 days. Net CO_2 assimilation and g_s were not reduced when plants without root rot were flooded for 7 days.**

In southern Florida, avocados are grown in calcareous soils [primarily Rockdale fine sandy loam (FSL)]. In these soils, damage caused by phytophthora root rot is particularly severe after avocado trees are flooded (Ploetz and Schaffer, 1988). Previous studies of root rot in avocado indicated that reductions in net CO_2 assimilation (A) and stomatal conductance for CO_2 (g_s) are among the earliest measured responses to flooding and root rot, and that these reductions precede the more conspicuous symptoms of root rot, such as wilting and defoliation, by 2 or more days (Ploetz and Schaffer, 1987, 1988; Schaffer and Ploetz, 1987). Thus, gas exchange characteristics are sensitive measures of host stress for this pathosystem.

In previous work, A and g_s were always reduced greatly when root-rotted plants were flooded, but were not reduced consistently when root-rotted plants were not flooded (Ploetz and Schaffer, 1987, 1988). Since only moderate severities of root rot (40% to 55%) were tested, it is not known what effect lower or higher severities of root rot have on flooded and nonflooded plants. Damage thresholds for phytophthora root rot of avocado under flooded and nonflooded conditions would provide valuable information about the epidemiology of this disease and the interaction of root rot and flooding. Our objective for this study was to determine damage thresholds for avocado trees with phytophthora root rot under flooded and nonflooded conditions by using A and g_s as physiological indicators of host stress.

Grafted avocado plants were used in two greenhouse studies: 'Simmonds' scions on seedling rootstocks from 'Lula' were used in the first experiment and 'Simmonds' scions on seedling rootstocks from 'Waldin' were used in the second one. Experiments 1 and 2 were conducted from April through July 1987 and 1988, respectively. A range of root rot severities (damage) was obtained by transferring plants grown in peat–perlite potting mix (Promix; Premier Brand, New Rochelle, N.Y.) in 10-cm-diameter (1 liter) pots to 20-cm-diameter (4 liters) pots filled with Rockdale FSL artificially infested with one of eight levels of inoculum (0.003, 0.03, 0.08, 0.31, 0.78, 1.56, 2.34, or 4.44 g of inoculum per liter of soil); a ninth treatment was not infested. Each treatment consisted of eight plants, potted individually. For the infested treatments, inoculum consisted of sorghum seed (Expt. 1) or oatmeal (Expt. 2) colonized by an isolate of *P. cinnamomi* used in previous studies (Ploetz and Schaffer, 1987, 1988; Schaffer and Ploetz, 1987).

Two months after transplanting, one-half of the plants for each treatment were flooded by placing pots in fiberglass reservoirs filled with tap water such that soil in the pots was ≈1 cm below the surface of the water. Thus, four plants from each inoculum level were flooded. Three plants with different inoculum levels were randomly placed in each reservoir. However, care was taken not to flood heavily infested plants in the same reservoir as plants with low inoculum levels; thus, *P. cinnamomi* from heavily infested treatments was prevented from contaminating plants infested with lower inoculum levels. Plants were flooded for 1 week, after which a subjective wilt rating (1 = no wilting and 5 = permanently wilted) was used to rate each plant (Expt. 2).

Gas exchange determinations in Expt. 1 were made 7 days after flooding in the laboratory in an open system as described by Ploetz and Schaffer (1988). Net CO_2 assimilation was determined with a Beckman model 865 infrared gas analyzer. Transpiration was determined with a dewpoint hygrometer (General Eastern Instruments Corp., Watertown, Mass), and g_s was calculated from transpiration. The leaf chamber was held at 31 ± 2C, which is optimal for avocado (Scholefield et al., 1980), and 50% ± 5% RH. In Expt. 2, net CO_2 assimilation, g_s, and substomatal CO_2 concentration (Ci) were determined 7 days after flooding by enclosing 6.25 cm^2 of the third fully expanded leaf from the apex of each plant in a Parkinson leaf chamber connected to a portable field gas and water vapor exchange analyzer (LCA-2, Analytical Development Co., Inc., Hoddesdon, Herts, U.K.). Outside air, containing 340 ± 10 μmol CO_2/mol and dried to a constant 20% RH, was pumped into the chamber at 0.375 liters·min^{-1}. Chamber air temperature was 31 ± 1C. All determinations in the greenhouse and laboratory were made at photosynthetic photon fluxes exceeding photon saturation (>700 μmol·s^{-1}·m^{-2}) (Scholefield et al., 1980). Photon levels in the laboratory were provided by four 500-W reflector flood lamps; greenhouse determinations used sunlight. Net gas exchange calculations were those described by

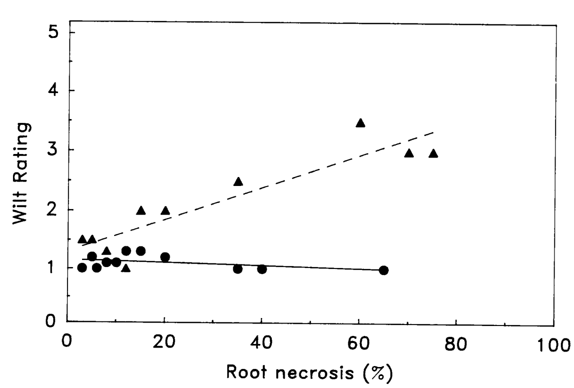

Fig. 1. Wilt rating (1 = no wilt; 5 = permanently wilted) and percent root necrosis for flooded (▲---▲) and nonflooded (●—●) avocado plants. Each datum represents the mean wilt rating for a given level of root necrosis. The regression line for flooded plants is $y = 1.31 + 0.03x$ ($r^2 = 0.94$, $P < 0.01$). The regression equation for nonflooded plants was not significant ($P < 0.01$).

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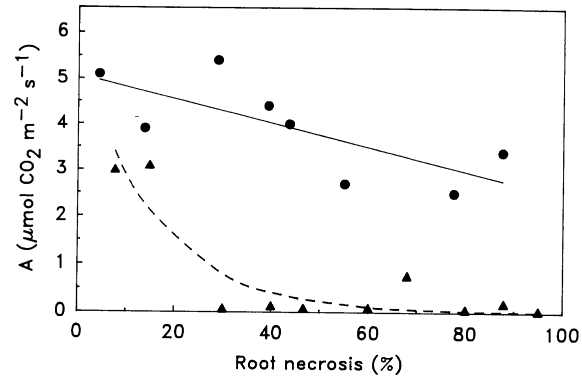

Fig. 2. Net CO_2 assimilation (A) and percent root necrosis for flooded (▲---▲) and nonflooded (●—●) avocado plants. Each datum represents mean A for a given level of root necrosis. The regression line for flooded plants is $y = 5.6e^{-065x}$ (r^2 = 0.83). The regression line for nonflooded plants is $y = 5.1 - 0.26x$ (r^2 = 0.53). Both regressions were significant at $P < 0.01$.

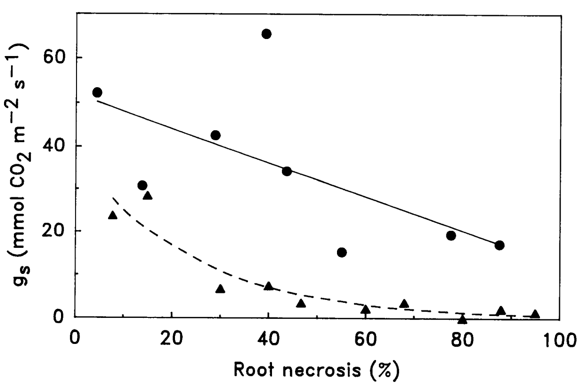

Fig. 3. Stomatal conductance for CO_2 (g_s) and percent root necrosis for flooded (▲---▲) and nonflooded (●—●) avocado plants. Each datum represents mean g_s for a given level of root necrosis. The regression line for flooded plants is $y = 38.5e^{-0.043x}$ (r^2 = 0.88). The regression line for nonflooded plants is $y = 52.0 - 0.40x$ (r^2 = 0.41). Both regressions were significant at $P < 0.01$.

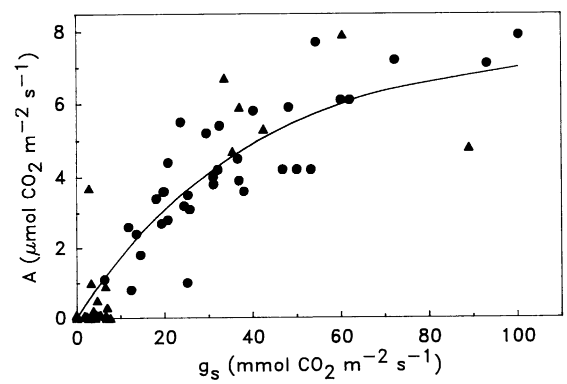

Fig. 4. Net CO_2 assimilation (A) and stomatal conductance for CO_2 (g_s) for flooded (▲) and nonflooded (●) avocado plants. The regression line for flooded and nonflooded plants combined is $y = 7.57(1 - c^{-0.026x})$ (r^2 = 0.85, $P < 0.01$).

Jarvis (1971) and von Caemmerer and Farquhar (1981).

Within 2 hr after determining leaf gas exchange, soil was removed from the root systems by gentle washing under running water. Percent necrosis for the entire root system was estimated visually for each plant, and the percentage of necrotic roots colonized by *P. cinnamomi* was determined in assays on a selective agar medium as described by Ploetz and Schaffer (1987). Percent root necrosis due to infection by *P. cinnamomi* was estimated by multiplying total percent root necrosis by the percentage of necrotic roots colonized by the pathogen.

Separate gas exchange determinations were made for flooded and nonflooded plants. Initial inoculum density was not highly correlated with percent root necrosis (data not shown). Since percent root necrosis provided a more accurate indication of damage than the inoculum level added to the soil, percent root necrosis, rather than inoculum density, was used as the dependent variable for statistical analysis. Thus, for statistical analysis, replicates were considered to be plants with the same percentage of root necrosis for flooded and nonflooded plants. The relationships between percent root necrosis and net gas exchange characteristics were analyzed by model II linear and nonlinear regression (Little and Hills, 1978).

Phytophthora cinnamomi was recovered frequently from most of the necrotic roots of plants grown in infested soil, but was never recovered from plants in noninfested soil. Since gas exchange responses of avocado to phytophthora root rot and flooding were similar in both experiments, gas exchange data are reported only for the first experiment.

Plants with root rot began to wilt 4 days after flooding was imposed. After 7 days, 41% of these plants had wilt ratings ≥2, whereas none of the nonflooded plants had wilt ratings >1.5. Wilt ratings were correlated with percent root necrosis for flooded plants (r^2 = 0.95), but not for nonflooded plants (Fig. 1).

Net CO_2 assimilation and g_s were decreased dramatically when plants with root necrosis ≥20% were flooded (Figs. 2 and 3). Host response under flooded conditions was described by the model: $y = ae^{-bx}$ (Figs. 2 and 3; r^2 = 0.83 and 0.88, respectively). Host response under nonflooded conditions was linear (Figs. 2 and 3; r^2 = 0.53 and 0.41, respectively). Reductions in A and g_s under nonflooded conditions were not as abrupt as under flooded conditions and were never greater than ≈65% of the maximum rates detected for plants in the noninfested treatment, even when root necrosis approached 90%. Davison and Tay (1987) observed that, under flooded conditions, g_s of eucalyptus (*Eucalyptus marginata* Donn. ex Sm.) infected with *P. cinnamomi* was lower than that of infected, nonflooded plants. They also observed that infected plants that were flooded wilted more rapidly than noninfected, flooded plants. Apparently, the sensitivity of avocado and eucalyptus to root rot caused by *P. cinnamomi* is increased under flooded conditions.

There was a positive curvilinear relationship between A and g_s when responses for flooded and nonflooded plants were combined (Fig. 4). Net CO_2 assimilation and g_s of flooded plants with >20% root necrosis were <1.25 μmol·s^{-1}·m^{-2} and 10 mmol·s^{-1}·m^{-2}, respectively; flooded plants represented in the middle of the regression line had <20% root necrosis (Fig. 4).

It has been suggested that flooding causes a reduction in g_s initially, which, in turn, limits the amount of CO_2 in the leaf (Davies and Flore, 1986b; Phung and Knipling, 1976). Reductions in A and g_s caused by flooding or disease have been correlated with several variables, including reduced hydraulic conductivity of the stem and/or roots (Andersen et al., 1984; Crane and Davies, 1987; Syvertsen et al., 1983), reduced capacity of plants to absorb water via the roots (Sterne et al., 1978), reduced mineral uptake under low soil O_2 tension (Slowick et al., 1979), and characterized or noncharacterized biochemical signals (Cahill et al., 1986; Davies and Flore, 1986b; Jackson and Hall, 1987; Sojka and Stolzy, 1980).

Reductions in A and g_s appeared to occur simultaneously in previous studies with avocado and phytophthora root rot in our laboratories (Ploetz and Schaffer, 1987, 1988; Schaffer and Ploetz, 1987), although the relationship between these two variables was not investigated. Davies and Flore (1986a, 1986b) found that reductions in residual conductance of blueberries subsequent to flooding resulted in increased Ci. Farquhar and Sharkey (1982) suggest that Ci and g_s should decrease together if g_s were limiting A. In contrast, an increase in Ci as g_s decreased would suggest that decreased A is causing decreased g_s. Therefore, determinations of Ci for flooded and nonflooded avocados with root rot could indicate whether reduced g_s or A is the earlier host response to flooding and root rot.

In the present study, g_s was always <100 $mmol \cdot s^{-1} \cdot m^{-2}$ under flooded conditions when root necrosis was $\geq 30\%$ (Fig. 4). Since A and g_s were positively correlated at g_s values <100 $mmol \cdot s^{-1} \cdot m^{-2}$ under flooded and nonflooded conditions, it is possible that g_s is limiting A in avocados with phytophthora root rot (Fig. 4). However, because Ci increased under these conditions (data not shown), a reduced photosynthetic capacity of plants with root rot may instead cause a reduction in g_s. If g_s were limiting A, a reduction instead of an increase in Ci would be expected, since there would be increased resistance to CO_2 entering the leaf (Farquhar and Sharkey, 1982). Davies and Flore (1986a, 1986b) reported reductions in A and g_s and a reduction in Ci within 24 hr after blueberry plants were flooded, thereby supporting their hypothesis that g_s limits A in blueberries under these conditions. However, they observed a subsequent decrease in residual conductance that resulted in increased Ci a few days after flooding. In our study, gas exchange was not determined until 1 week after flooding was imposed, and residual conductance was not determined. Therefore, it is possible that sequential observations of flooded avocado plants may detect an initial decrease followed by an increase in Ci due to root rot. Additional research is needed to determine the relationships among A, g_s, and Ci for flooded and nonflooded avocado plants infected with *P. cinnamomi*.

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Screening with Ethephon for Abscission Resistance of Flower Buds in Bell Pepper

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Abstract. **Under conditions of environmental stress, many pepper (*Capsicum annuum* L.) cultivars lose flower buds, probably due to production of the abscission-causing hormone ethylene. Field applications of the ethylene-generating chemical ethephon (0 to 300 $\mu l \cdot liter^{-1}$) were made to five cultivars of bell pepper growing under nonstressed conditions, but differing in resistance to stress-induced bud abscission. Cultivars were seeded at several times in 1985 to synchronize stages of plant development and allow a single simultaneous spray application to all plots. In the two 1986 experiments, all cultivars were sown on the same date and either two or three sprays were applied to all plots to more closely approximate screening conditions used by plant breeders. One week after application of ethephon at 300 $\mu l \cdot liter^{-1}$, virtually no flower buds remained on any cultivar in either year. Susceptible cultivars exhibited significantly greater abscission than resistant ones at ethephon concentrations of 75 to 200 $\mu l \cdot liter^{-1}$. The use of ethephon shows promise as a simple screening method for resistance to stress-induced flower bud abscission in pepper. Chemical name used: 2-chloroethyl phosphonic acid (ethephon).**

A wide variety of conditions may induce floral abscission in bell pepper, with high temperature being most frequently implicated (1, 5, 7). Cochran (1) found that drought also increased floral abscission, particularly at high temperatures (27/21C day/night vs. 21/16). Irradiance that is either too low (7) or too high (6), and low N status (1), may also favor abscission. Hernandez-Armenta (2) found that bud abscission contributed more to fruit set reduction in peppers than did flower or fruit abscission, and that there were significant cultivar differences in bud abscission.

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