Effect of Phytophthora Root Rot on Water Relations of Avocado: Interpretation with a Water Transport Model

R. E. Sterne, M. R. Kaufmann, and G. A. Zentmyer

Graduate Research Assistant, Department of Plant Pathology, Associate Professor, Department of Plant Sciences, and Professor, Department of Plant Pathology, University of California, Riverside, CA 92502, respectively. Present address of the senior author: Department of Plant Pathology, University of Arkansas, Fayetteville, AR 72701. Present address of second author: U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO 80521.

Supported in part by National Science Foundation Grant Nos. PCM76-01128 to M. R. Kaufmann, PCM74-19982 to G. A. Zentmyer, and by a California Avocado Advisory Board grant to G. A. Zentmyer.

Accepted for publication 22 September 1977.

ABSTRACT

STERNE, R. E., M. R. KAUFMANN, and G. A. ZENTMYER. 1978. Effect of Phytophthora root rot on water relations of avocado: Interpretation with a water transport model. Phytopathology 68: 595-602.

A field study was conducted to compare the water relations of healthy avocado trees and trees with roots naturally infected with Phytophthora cinnamomi. Data for diurnal fluctuations in stomatal behavior (measured as leaf conductance of water vapor), transpiration, and water stress for well-watered healthy and diseased trees are presented. A water flux model of the soil-plant-atmosphere continuum was used to examine data on leaf xylem pressure potential (determined by the pressure chamber method) and transpiration for healthy trees (well-watered and waterstressed) and for diseased trees. Values of leaf conductance and transpiration were higher throughout the day in nonstressed healthy trees than in those with Phytophthora root rot. Daytime and nighttime values of xylem pressure potential were lower in diseased trees than in healthy trees; the lowest potentials were -13 to -14 bars and -9 to -11bars, respectively. Xylem pressure potential at night (zero transpiration) averaged -1.8 bars and -7.0 bars in

For an evaluation of the effect of Phytophthora root rots on host plants, information is needed on the plant and soil water relationships of healthy and diseased plants. The symptoms of root rot of avocado caused by *Phytophthora cinnamomi* Rands (15) resemble water stress; i.e., wilting, leaf discoloration, die-back, and reduced reproductive growth (12, 14). Smith noted (12 that the arbitrary division of stress factors into pathological and nonpathological groups is unfortunate because the division leads to the impression that the factors operate independently of one another, while in fact, plant water stress depends upon dynamic interactions between environmental, biotic, and plant factors that influence water supply and development of water stress in plants.

The soil-plant-atmosphere continuum model for water transport first described by van den Honert (5) provides a useful theoretical basis for examining plant-environment interactions. According to the model, under steady-state conditions water flux from the soil through the plant to the atmosphere can be expressed as a series of gradients

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nonstressed and water-stressed trees, respectively, and -8.0 bars in diseased trees. There was a consistent relationship between xylem pressure potential and transpiration in leaves of nonstressed avocado trees; i.e., changes in transpiration were accompanied closely by changes in xylem pressure potential. However, the relationship in diseased trees resembled the relationship in water-stressed trees: it was inconsistent and varied with the time of day. At a given transpiration rate in the afternoon, xylem pressure potential in diseased trees was considerably lower than with equivalent transpiration in the morning. The water flux model predicted that in diseased trees, low xylem pressure potential resulted from increased resistance to flow in the soil-plant system even in well-watered soil. A hypothesis for the increased resistance is given. Apparently, root disease caused by P. cinnamomi induced such major changes in the water transport system of avocado trees that typical plant control mechanisms (e.g., stomatal closure) could not correct the water deficits.

and resistances describing transport through each segment of the pathway for water flow.

$$Flux = \frac{\psi_{soil} - \psi_{root}}{r_{soil-to-root}} = \frac{\psi_{root} - \psi_{leaf}}{r_{root-to-leaf}} = \frac{\Delta Abs. Hum.}{r_{leaf-to-air}}$$
(Eq. 1)

where ψ is water potential, r is flow resistance, and ΔAbs . Hum. is the difference in absolute humidity between leaf and air.

Recently, considerable attention has been given to understanding how leaf water potential (ψ_{leaf} in Eq. 1) is influenced by soil and atmospheric factors (4, 6, 8, 9, 11). An equation that describes leaf water potentials as a function of these factors can be obtained from Eq. 1 (see ref. 8 for further details):

$$\psi_{\text{leaf}} = \psi_{\text{soil}} - \text{Flux} \times (r_{\text{soil-to-leaf}}) \quad (\text{Eq. 2})$$

According to this equation, leaf water potential is decreased by a reduction in soil water potential if the transpiration rate (flux) or resistance do not change. If flux or resistances to flow of water to the leaves is

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increased, a decrease in leaf water potential is predicted. Considerable evidence (reviewed in 8) is available to support Eq. 2 as a predictive model for leaf water potential. Thus, this simple model appears to be useful for interpreting how edaphic and atmospheric factors influence plant water stress.

Elfving et al. (4) used the water flux model as a means of interpreting leaf water potential measurements in Valencia orange trees. When soil matric potential was greater than -0.3 bar (i.e., nonlimiting for water absorption), changes in transpiration were accompanied by changes in leaf water potential such that, at similar transpiration rates in the morning and afternoon, equivalent water potentials occurred. The close linkage of leaf water potential to transpiration with a nonlimiting soil environment and contrasting climates was consistent with Eq. 2 and provided a basis for interpreting changes in leaf water potential with various edaphic conditions. For example, Eq. 2 predicts that when soil water potential decreases, leaf water potential will be lower at all transpiration rates than with nonlimiting soil conditions. However, if root permeability is decreased (increased $r_{\text{soil-to-leaf}}$), leaf water potential is expected to be lower compared with that at nonlimiting soil water potentials only when flux is above zero. Citrus data from the field and laboratory confirmed the model predictions (4).

Papendick and Campbell (11) used a water flow model similar to Eq. 1 to describe how vascular wilt fungi might cause changes in water relations of infected plants. They postulated that vascular wilt fungi increased the resistance to flow of water in xylem of infected plants (root-to-leaf in Eq. 1 and $r_{soil-to-leaf}$ in Eq. 2), resulting in lower leaf water potential than in healthy plants. In addition, they suggested that other factors, including low root volume caused by nutrient deficiency, and root damage from mechanical breakage or root diseases, might reduce plant water potential and cause water stress even when high water potentials existed in the soil.

This paper describes the results of a field study that compared the water relations of healthy avocado trees and trees infected with *Phytophthora cinnamomi*. During the experiments, some healthy trees were stressed for water by stopping irrigation treatments. Stomatal regulation of water loss and the effects of soil water status on water deficits in avocado trees are discussed in another paper (13). Data presented here compare diurnal fluctuations of water stress, stomatal behavior, and transpiration rates for healthy and diseased trees that were well-watered. The leaf water potential model described above is examined for its utility for interpreting differences in water stress and transpiration in: (i) healthy, well-watered trees, (ii) healthy, water-stressed trees, and (iii) diseased trees.

MATERIALS AND METHODS

Water relations data were collected from 8- to 10-yr-old avocado trees (*Persea americana* Mill. 'Bacon') growing in an inland valley orchard near Fallbrook in San Diego County, California. Data were taken on six healthy trees located in a grove of trees on a 5 to 9-degree north slope in a Visalia sandy loam soil. A group of trees infected with *P. cinnamomi* was separated along the contour about 20 m from the group of healthy trees. The infected trees were in a Las Posas fine sandy loam soil with a clay layer 60 cm thick beginning 30 cm below the soil surface. Root infection was confirmed by placing feeder roots from the trees on agar and observing subsequent growth of *P*. *cinnamomi* (15). The tops of the five diseased trees had an average disease rating of 2.5 on a scale where zero = healthy trees and 5 = dead trees. Sprinklers with fullrotating heads applied water locally near each tree.

Water relations data were collected from both healthy and diseased trees at intervals throughout July and August, 1976. Daytime plant and environment measurements were made every 2-4 hr from sunrise until sunset on the north and south sides of the trees. Nighttime data were taken at least 1 hr after sunset and 1-2 hr before sunrise. Leaf temperatures were estimated from leaf to air temperature difference measured with a Tshaped thermocouple clamp after Elfving et al. (4). Incident, photosynthetically active radiation (PAR, 400-700 nm wavelengths) was measured near leaf surfaces with a quantum sensor (Model LI-190S, Lambda Instruments Corp., Lincoln, NE 68504). Atmospheric and edaphic measurements included soil temperature (from a thermometer at 15 cm) and air temperature and relative humidity (from a wet and dry bulb psychrometer). The absolute humidity difference from leaf to air was estimated from leaf temperature and the external humidity by assuming that the air in a leaf is saturated with water. Soil water status was monitored using tensiometers located beneath the edge of the tree canopy and placed at depths of 30, 60, and 90 cm. Tensiometers do not adequately estimate soil matric potentials more negative than -0.8 bar; however, they are the instruments recommended for determining soil water status where avocado root rot occurs (15).

Paired measurements of leaf conductance and leaf xylem pressure potential were made on healthy and diseased avocado trees. Xylem pressure potential was measured by the pressure chamber method. In another paper (13), we showed that xylem pressure potential for avocado leaves provided an adequate estimate of leaf water potential. Leaf conductance of water vapor was measured with a diffusion porometer having a LiCl sensor mounted in an unstirred aluminum chamber (4). The porometer was calibrated with five perforated plates, each having a known resistance (7). Calibration was done at four temperatures representative of field conditions at the time of data collection.

To study water stress in healthy trees, we stopped irrigation on 11 trees, and soil matric potential, xylem pressure potential of leaves, and transpiration rates were monitored every 2-3 days (see ref. 13 for details of irrigation treatments). After 30 days, soil matric potential was less than -0.8 bar to 90 cm in soil beneath the trees. At that time, water relations data were collected for 48 hr from five trees in the center of the group of trees without irrigation.

RESULTS

For well-watered trees, edaphic conditions remained at levels determined empirically to favor maximum water absorption by the roots of avocado whether healthy or infected with *P. cinnamomi*. Healthy trees were irrigated for 4-6 hr every 7-8 days and diseased trees were irrigated 4 hr every 14-20 days. The irrigation applications maintained the soil water status beneath the trees at matric potentials from -0.1 to -0.3 bar at all depths measured. Soil temperatures ranged from 18 to 21 C throughout the study. The root environment beneath the trees was considered "nonlimiting" to water absorption (9).

Figure 1 and 2 show a typical diurnal fluctuation in the absolute humidity difference from leaf to air and leaf conductance of water vapor for nonstressed avocado trees and for trees infected with *P. cinnamomi*. The absolute humidity differences in Fig. 1 are representative of daytime and nighttime values that occurred throughout the study. Humidity differences were similar for leaves of diseased and healthy trees. Measurements of leaf conductance were taken only on the abaxial side of avocado leaves because porometer readings indicated that conductance was essentially zero on the adaxial side of leaves at any time of day or night.

For leaves of healthy trees with high PAR (sun leaves), leaf conductance increased from zero at night to 0.07-0.08 cm·sec⁻¹ at 0830 hours and remained near that level until

1800 hours; then conductance decreased to near zero at 2000 hours (Fig. 2). At low PAR (shade leaves), leaf conductance rose to approximately $0.05 \text{ cm} \text{ sec}^{-1}$ at 0830 hours and then decreased steadily throughout the day. For leaves of diseased trees, mean values of conductance were similar with low and high PAR, and were less than those for healthy trees with either level of light (Fig. 2). The highest conductance occurred at 0900 hours (0.03-0.04 cm sec⁻¹), then values decreased to approximately 0.015 cm sec⁻¹ at 1200 hours and remained near that level until sunset when they approached zero.

The product of leaf conductance of water vapor and the absolute humidity difference from leaf to air was used to estimate transpirational flux density of avocado leaves (13). For example, with high PAR the mean transpirational flux in the leaves of healthy trees at 1400 hours was $1.78 \ \mu g \ cm^{-2} \ sec^{-1}$ (Fig. 3). That flux density resulted from a leaf conductance at 1400 hours of 0.074 cm sec⁻¹ (Fig. 2, healthy trees, high PAR) and an absolute humidity difference of 24.05 $\mu g \ cm^{-3}$ (Fig. 1, high PAR). In healthy trees, transpirational flux peaked between 1200 and 1400 hours (Fig. 3). During those hours the

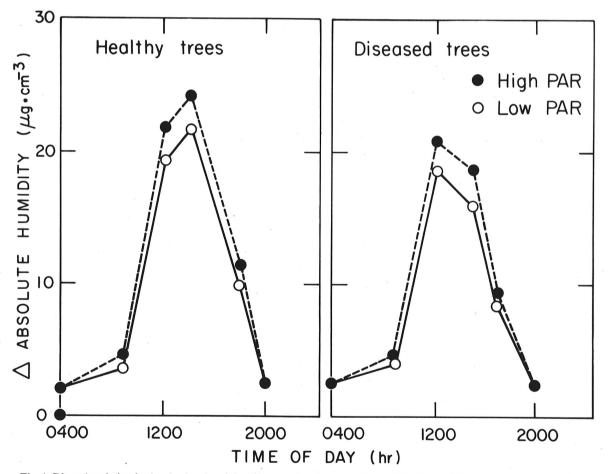


Fig. 1. Diurnal variation in the absolute humidity difference from avocado leaves of healthy and diseased avocado to ambient air with different levels of photosynthetically active radiation (PAR). High PAR = 168 to 210 nanoeinsteins cm⁻²·sec⁻¹. Low PAR = 4 to 13 nanoeinsteins cm⁻²·sec⁻¹. Absolute humidity differences estimated from leaf temperature and external humidity by assuming air in a leaf is saturated with water.

mean flux with high PAR ranged from 1.13 to 1.78 $\mu g \cdot cm^{-2} \cdot sec^{-1}$, and with low PAR the mean flux was between 0.45 and 0.57 $\mu g \cdot cm^{-2} \cdot sec^{-1}$. With either high or low PAR, transpirational flux was approximately the same throughout the day in the leaves of trees infected by P. cinnamomi (Fig. 3). In diseased trees, highest flux occurred between 1000 and 1200 hours and then transpiration decreased throughout the afternoon, presumably because of stomatal closure (Fig. 2). Porometer readings at night indicated that water was not evaporating from leaves of either healthy or diseased avocado trees. Therefore, conductance and transpiration were assumed to be zero from 1 hr after sunset until sunrise.

Throughout the day and night, leaf xylem pressure potential in healthy avocado trees was less negative (i.e., less water stress) than in trees infected with P. cinnamomi (Fig. 4). Xylem pressure potential in leaves of healthy trees was lowest between 1200 and 1500 hours, and was -9.0 to -11.0 bars and -7.0 to -8.0 bars for high and low PAR, respectively. The mean xylem pressure potential in healthy trees at night was -1.75 bars. For diseased trees, the nighttime xylem pressure potential averaged -8.0 bars (1-2 hr before sunrise). After sunrise, xylem pressure potential in diseased trees decreased steadily to a minimum of -14.0 bars at 1800 hours. In contrast, xylem pressure potential in healthy trees reached a minimum several hours earlier in the day, and by 1800 hours considerable recovery already had occurred.

For healthy trees having an adequate supply of soil

water, there was a close relationship between xylem pressure potential and transpirational flux density of the leaves (curve for healthy trees in Fig. 5). The data for simultaneous measurements of leaf xylem pressure potential and transpiration of healthy avocado trees are presented in another paper (13). During July and August, 1976, when the water relations data were collected, daytime atmospheric conditions ranged from hazy overcast to dry desert winds. However, regardless of the climatic conditions, level of PAR, or the time of day when readings were made, leaf xylem pressure potential decreased and increased with fluctuations in transpirational flux. In other words, as transpiration increased in nonstressed trees, xylem pressure potential decreased in a predictable manner, and at an equivalent transpiration rate, xylem pressure potential was similar in the morning and afternoon. The curves for healthy trees presented in Fig. 5 were plotted from a logarithmic equation (base 10); the regression coefficient was -0.93and the 95% predictive confidence interval was \pm 1.9 bars. In leaves with low PAR, transpiration rates did not exceed 0.70 $\mu g \cdot cm^{-2} \cdot sec^{-1}$ and xylem potential was not lower than -10 bars. With high PAR, xylem pressure potential was as low as -11 bars when transpirational flux approached 1.6 μ g·cm⁻²·sec⁻¹. However, for comparison with xylem pressure potentials and transpiration in infected trees, the curve in Fig. 5 only shows xylem potentials corresponding to transpirational flux as high as 1.0 μ g·cm⁻²·sec⁻¹ in healthy trees.

In trees stressed by low soil water potential and in trees

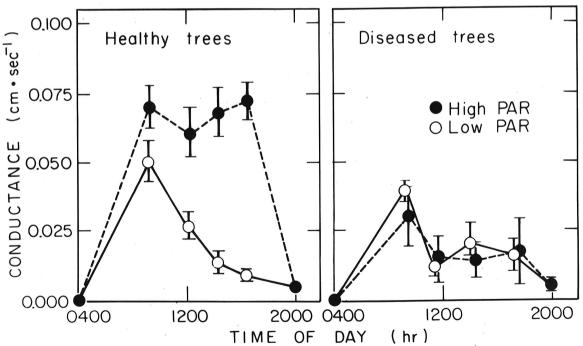


Fig. 2. Effect of high and low levels of photosynthetically active radiation (PAR) and root disease caused by Phytophthora cinnamomi on diurnal fluctuations in conductance of water vapor by avocado leaves. Healthy and diseased trees were well-watered (soil matric potential > -0.3 bar). High PAR = 168 to 210 nanoeinsteins cm⁻² sec⁻¹. Low PAR = 4-13 nanoeinsteins cm⁻² sec⁻¹. Each point represents the mean of six to eight measurements of leaf conductance; bars represent \pm standard error.

infected with P. cinnamomi the response of xylem pressure potential to transpirational flux differed sharply from the response observed in healthy trees (Fig. 5). In leaves of water-stressed and diseased trees with either high or low PAR there was no longer a consistent diurnal relationship between xylem pressure potential and transpirational flux. Instead, the relationship depended upon the time of day as indicated by numerals in Fig. 5. For leaves of water-stressed and diseased trees, xvlem pressure potential was more negative at a given transpiration rate in the afternoon than the potential at the same transpiration rate in the morning; i.e., the system exhibited hysteresis. After 1000 hours, transpiration in infected trees began to decrease, but xvlem pressure potential continued to decrease steadily until approximately 2000 hours when the sun was setting and transpiration approached zero.

One diseased tree had less severe symptoms (disease rating 1) than the other four diseased trees and the water relations data from that tree indicated that water stress was less extensive during the day and night. Throughout diurnal cycles, xylem pressure potential in the tree with the low rating was intermediate between that of healthy trees and that of trees with higher disease ratings. Transpiration rate was higher in the afternoon (1200 to 1700 hours) than in the severly diseased trees and xylem pressure potential was never below -11.5 bars.

DISCUSSION

Infection by P. cinnamomi induced changes in the water relations of avocado trees that resulted in severe plant water stress that resembled stress caused by low soil water potential. Several important parameters, including leaf conductance of water vapor, transpiration, and leaf xylem pressure potential were altered considerably in infected trees (Fig. 2, 3, and 4). Leaf xylem pressure potential was lower during the day and night than in healthy trees. A large number of physiological processes in plants depend on leaf water potential (8, 9, 10) and reductions in vegetative and reproductive growth of trees are highly correlated with water stress induced by changes in the atmospheric and edaphic environments (12, 14). In addition, many of the symptoms of disease caused by root rotting organisms can be related to alterations in water relations parameters of the host plant (2, 11). In the case of avocado trees infected by P. cinnamomi, low xylem pressure potential (an estimate of leaf water status) during the day and night was probably the primary factor involved in the symptoms of stress; i.e., wilt, die-back, and reduced growth and productivity.

Equation 2 shows that leaf water potential is not an independent variable that controls water flow through a plant. Rather it depends upon the water supply to the plant and on transpirational flux; it integrates edaphic,

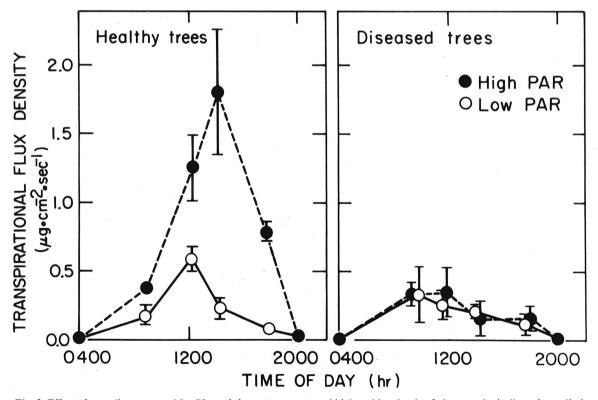


Fig. 3. Effect of root disease caused by *Phytophthora cinnamomi* and high and low levels of photosynthetically active radiation (PAR) on diurnal changes in transpirational flux density of avocado leaves. Healthy and diseased trees were well-watered (soil matric potential > -0.3 bar). High PAR = 168 to 210 nanoeinsteins cm⁻² sec⁻¹. Low PAR = 4-13 nanoeinsteins cm⁻² sec⁻¹. Each point represents the mean of six to eight measurements of transpiration; bars represent \pm standard error. Transpirational flux density estimated as the product of water vapor conductance and the absolute humidity difference from leaf to air.

atmospheric, and physiological effects on water flux through a plant (8, 9). The close linkage and consistent relationship between xylem pressure potential and transpirational flux in the leaves of well-watered avocado trees (13, and Fig. 5) agreed with a major assumption of the model for water transport (Eq. 1 and 2); i.e., with nonlimiting soil water conditions, xylem pressure potential varies in a predictable manner with

transpiration. Therefore, Eq. 2 could be used to predict and interpret changes in xylem pressure potential that might occur when trees were stressed for water by either pathological or nonpathological factors. For several woody perennials (8) reductions of the

water potential of the soil caused a decrease in leaf water potential. This observation is consistent with Eq. 2 which predicts that as soil dries (ψ_{soil} is reduced), the potential of water in the leaves will be lower at all transpiration rates than the potential that occurred with nonlimiting conditions. Even at night when transpiration is minimal, leaf water potential should be lower. In addition, soil-toleaf resistance ($r_{soil-to-leaf}$ in Eq. 2) might also increase as soil dries because soil hydraulic conductivity (inversely related to flow resistance) can decrease sharply. Other factors may increase resistance in roots such as damage to the cortical cells of a root during periods of stress caused by low water potential of the soil (8).

We hypothesized that Phytophthora root rot would influence leaf xylem pressure potential primarily through the resistance term ($r_{soil-to-leaf}$) in Eq. 2 (see ref. 2). The equation predicts that high soil-to-leaf resistance would only affect leaf water potential when flux is greater than zero. At night with no transpiration, xylem pressure potential is not predicted to differ greatly from the potential at zero transpiration in healthy trees in nonlimiting soil conditions. Therefore, we expected that water stress in diseased trees might be characterized by a steeper slope in the response curve of leaf xylem pressure potential to transpiration than the slope of the curve with nonlimiting soil conditions. The steeper slope would result directly from increased resistance to the flow of

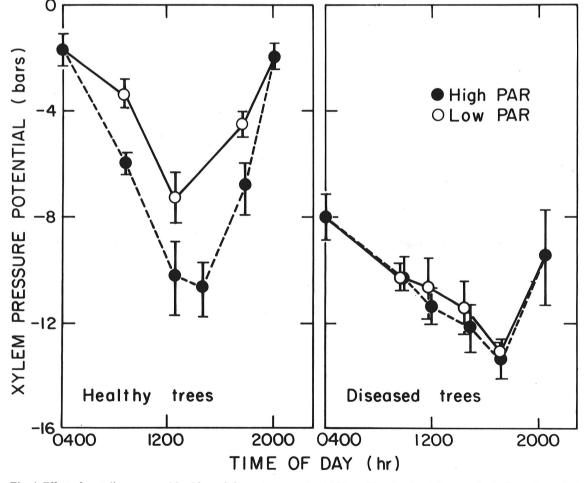


Fig. 4. Effect of root disease caused by *Phytophthora cinnamomi* and high and low levels of photosynthetically active radiation (PAR) on diurnal changes in xylem pressure potential of avocado leaves. Healthy and diseased trees were well-watered (soil matric potential > -0.3 bar). High PAR = 168 to 210 nanoeinsteins $cm^{-2} sec^{-1}$. Low PAR = 4-13 nanoeinsteins $cm^{-2} sec^{-1}$. Each point represents the mean of six to eight measurements of leaf xylem pressure potential; bars represent \pm standard error.

water in the soil-plant system of diseased trees.

The low nighttime levels of xylem pressure potential and the nature of the water stress we found in diseased trees were unexpected. The low values indicated that, even when transpiration was zero, insufficient water moved from the bulk of the soil where supply of water was adequate to permit recovery during the night period. Clearly, the number of absorbing roots of infected trees was reduced. We now believe that a reduction in the number of absorbing roots of diseased trees placed excessive demands on the remaining healthy roots to absorb water when transpiration was high. Under those circumstances, soil water content close to absorbing roots would be reduced sharply below that in bulk of the soil, and severely reduced hydraulic conductivity would curtail nighttime recovery (11). Furthermore, the remaining roots were presumably older and suberized, thus were limited in capacity for water absorption, even in

saturated soil. Perhaps equally important is a serious daytime reduction in stored water content within the plant. Recharge of the water storage volume at night, necessary for recovery of leaf water potential, may be inadequate because of limited absorption by the root system. Apparently the situation in the rhizosphere of diseased trees mimicked dry soil conditions that depress leaf water potential in healthy trees even when transpiration is minimal (Fig. 5 and ref. 13).

The hysteresis in the response curve of leaf xylem pressure potential to transpiration in water-stressed and infected trees indicated that xylem pressure potential was not coupled with transpirational flux (Fig. 5). In diseased trees, even though transpiration decreased after 1000 hours, xylem pressure potential decreased steadily until very late in the afternoon (1700 hours). In nonstressed trees xylem pressure potential increased and decreased in a consistent relationship with transpiration and the

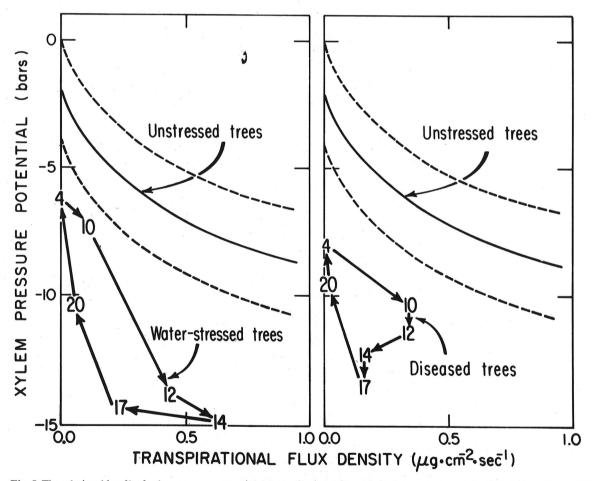


Fig. 5. The relationship of leaf xylem pressure potential to transpirational flux density in leaves of avodado trees (irrigated every 7-8 days), of water-stressed trees (without irrigation for 30 days), and of trees infected by *Phytophthora cinnamomi*. Photosynthetically active radiation (PAR) = 168 to 210 nanoeinsteins cm⁻² sec⁻¹. The solid line for healthy trees was plotted from a logarithmic (base 10) regression equation $\{y = -8.65 - 6.73 [log (x + 0.1)]\}$ developed from 110 individual data points; dashed lines indicate confidence limits, P = 0.05. Data from healthy trees at high and low PAR fitted the same curve. For water-stressed and infected trees, numbers indicate time of day of measurement (e.g., 4 = 0400 hours); each number is the mean of eight to ten measurements of xylem pressure potential and transpiration.

curvilinear response curve for healthy trees suggested that resistance to flow (the slop of the curve) actually decreased as transpiration increased. The steady reductions in xylem pressure potential in diseased trees, even when transpiration decreased, indicated that resistance to water flow ($r_{soil-to-leaf}$) increased throughout the day even though soil water status in the bulk soil was nonlimiting to water absorption. Apparently, infection by *P. cinnamomi* induced such major changes in the soilto-leaf water transport system that typical physiological controls of water loss from plants could not correct the water deficits that developed in infected avocado trees (1).

Overall, the symptoms of avocado root rot appear to be closely related to the effects of water stress on the plant as indicated by changes in xylem pressure potential of leaves. Water relations data for a diseased tree with a low disease rating indicated that water stress was not as intense as in trees with more severe symptoms of disease. Our observations on the water relations of healthy and diseased avocado illustrated that a model of water transport can be used to predict and explain the complex water relations of plants stressed by low soil matric potential and by disease caused by a root pathogen.

Duniway (2, 3) found that root disease of safflower plants caused by Phytophthora drechsleri increased resistance to water uptake through the root system and also greatly increased resistance to water movement through the xylem in stems. He pointed out that the role of a fungal toxin in the resistance to flow in diseased plants had not been studied and it was not even known whether increased resistance in root or xylem tissue was a specific response to infection by P. drechsleri or a more general response to root injury. At present, no toxins have been reported for P. cinnamomi and there is no information on resistance to water movement in different parts of plants whose roots are infected. The results of this investigation illustrated the extent and nature of water stress in diseased plants, but a complete evaluation awaits precise information on the mechanisms by which root pathogens induce plant water stress.

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