

Changes in Resistance to Water Transport in Safflower During the Development of *Phytophthora* Root Rot

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ABSTRACT

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Resistances to the movement of liquid water through healthy safflower plants and safflower plants infected with *Phytophthora cryptogea* were measured at various times after root inoculation. Healthy plants had a total resistance of 7×10^3 bars \cdot sec \cdot cm⁻¹ and 44, 13, and 43% of the resistance in healthy plants was located in the roots, stems, and leaves, respectively. During the development of *Phytophthora* root rot in safflower, the resistance of both the roots and stems increased progressively, but the resistance to water movement in leaves remained unchanged. By the time infected plants wilted, 5 days after inoculation, resistances of

infected roots and stems were more than 8 and 40 times the respective resistances in healthy plants. Measurements of transpiration rate and leaf water potential in intact plants showed that increased root and stem resistances to water movement accounted for the depressions of water potential and wilt symptoms that occurred in infected plants. At all stages of disease development, the influence of infection on root resistance greatly exceeded the influence of infection on the size of root systems. Increases in the xylem resistance of infected plants extended up the stem into internodes from which the pathogen was not isolated.

Additional key words: water relations, *Phytophthora drechsleri*, *Carthamus tinctorius*.

There is presently very little information on the mechanisms by which root pathogens alter the water relations of their hosts (7). A root pathogen may damage the host primarily because it decreases root density and distribution in the soil, thereby decreasing the ability of the plant to extract water from the soil. Accordingly, reductions in the size of root systems are sometimes used to estimate the damage induced by root pathogens, and there is the implication that adequate soil water can help compensate for the loss of functional roots. On the other hand, a root pathogen may alter the water relations of the host more directly, by changing resistance to water uptake, or other water-related parameters within the plant.

A previous paper (5) presented evidence that wilting of safflower plants with *Phytophthora* root rot is due to an unusually large resistance to water uptake within infected plants. Resistances to water uptake in safflower were examined by measuring rates of recovery from water stress (5). Although the recovery experiments clearly demonstrated that *Phytophthora* root rot greatly increased resistance in the roots and stem, the complex geometry and kinetics of recovery precluded quantitative estimates of resistance to water flow (5). Quantitative estimates of resistance would enable one to evaluate more fully the impact of various pathogen-induced resistances on the water status of the plant. The present paper describes the use of steady-state techniques to

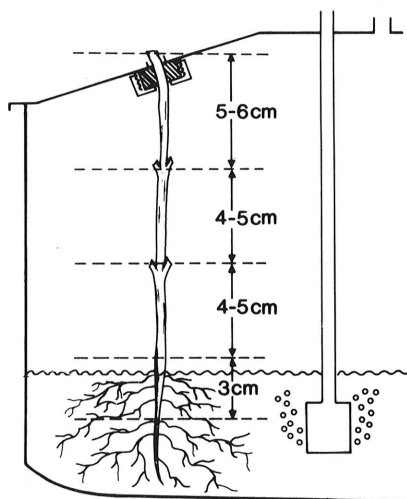
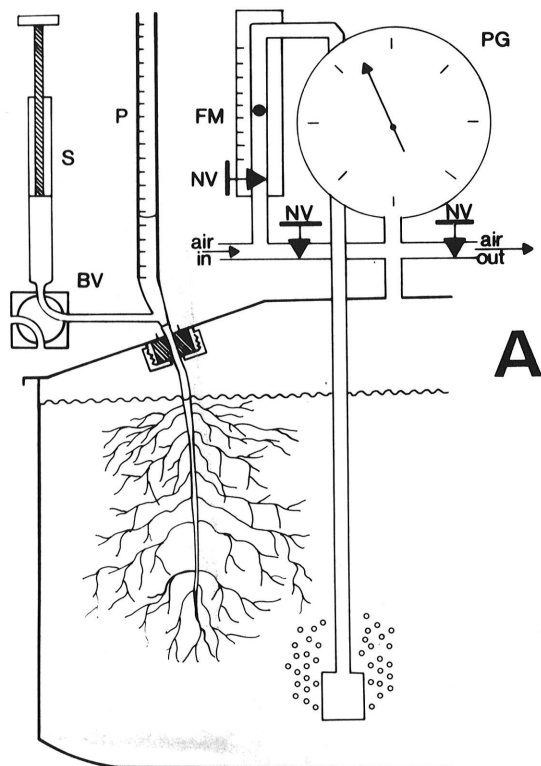
quantitatively examine resistances to water flow through the roots, stems, and leaves of safflower plants with *Phytophthora* root rot.

MATERIALS AND METHODS

Biological materials.—Safflower plants (*Carthamus tinctorius* L. 'Nebraska 10') were grown in solution-culture by the methods described previously (5). Plants were grown in a greenhouse at 25 C and 3 wk after seeding they were moved into a controlled-environment chamber having 85 W \cdot m⁻² (wavelength range, 300-700 nm) of light for 14 hr/day at 27 ± 0.1 C and $75 \pm 3\%$ relative humidity. Four-week-old plants were inoculated by pipetting 2×10^6 motile zoospores of *Phytophthora cryptogea* Pethyb. and Laff. into each container of nutrient solution. The same isolate of *P. cryptogea* (P201) was used previously under the name *P. drechsleri* Tucker (5). However, its morphology fits the description of *P. cryptogea* more closely than the description of *P. drechsleri* (6). A darkening of root tips 1-2 days after inoculation was the first visible symptom of infection. Wilting, which was the predominant symptom in the tops of infected plants, usually occurred 5-7 days after inoculation.

Resistance to water flow.—Each daily measurement was done simultaneously on one healthy and one infected plant between 900 and 1300 hours. The areas of all leaves (one surface only) were traced on paper and measured with a planimeter. The stems were cut just below either

the cotyledons or the second pair of adult leaves above the cotyledons (the first four to six leaves of safflower tend to be in opposite pairs). The lower stems and roots were promptly placed in a pressure apparatus similar to the one used by Mees and Weatherley (13), made from a 12-liter steel tank normally used for spray painting. The position of stems and roots and the major components of the pressure apparatus are illustrated (Fig. 1). The pressure apparatus was filled to the level of the highest branch roots with nutrient solution and air was bubbled through the solution at a constant rate of 300 cm³ per minute.



Pressures of 1-4 bars (± 0.05 bar) were applied to the nutrient solution and the resulting rates of water flow through the roots and stems were measured. Each measurement required 1-5 min and measurements of flow were done periodically while the pressure was maintained constant for 30-60 min. Root temperatures were 23-26 C during the measurements. The solute potentials (ψ_s) of the solution that passed through roots, and of the nutrient solution in which roots were immersed, were determined with a thermocouple psychrometer (5). After the measurements were completed, the roots were blotted dry and weighed.

Resistances to water flow through stem segments also were measured in those plants that were cut at the second pair of adult leaves for the pressure apparatus (Fig. 1-B). At the conclusion of the measurements on roots already described, the pressure apparatus was opened, the bubbler was removed, and the nutrient solution was replaced with freshly boiled water at 25 C. Roots were cut under water 3 cm below the highest branch root (Fig. 1-B) and the pressure apparatus was used to apply a total pressure difference of 0.1 ± 0.005 bar. Flow upwards through the segments was periodically measured for 20 min. The pressure apparatus was reopened, the level of boiled water was raised, and the stem was cut under water at the level of the highest branch root. A pressure difference of 0.1 bar was again used to measure rates of flow. The entire procedure was repeated until the roots and stems had been progressively cut for measurements of water flow at all of the levels shown by dashed lines in Fig. 1-B. The segments of stem between cuts were numbered from the roots up. In some experiments, a dilute solution of basic fuchsin (3) rather than water was used on cut segments in the pressure apparatus. The midportions of stained segments were cut into thin sections and radii of all xylem elements were measured under a microscope (3). *Phytophthora cryptogea* was isolated from the root and stem segments by the methods used previously (5).

The influence of heating the roots of noninoculated plants on resistance to water flow was examined in one set of experiments. Roots of 4-wk-old plants were immersed in water at 100 C for 30 sec. Only roots more than 5 cm below the origin of the highest branch roots

Fig. 1-(A,B). Pressure apparatus used to measure resistances to water flow in roots and stems of healthy safflower plants and safflower plants infected with *Phytophthora cryptogea*. The apparatus is shown in partial cross sections with A) stem and roots excised at the cotyledons and B) at the second pair of adult leaves. Two plants (one infected and one healthy) were simultaneously placed in the apparatus in comparable positions and pressure-tight seals were made around the stems. The desired pressure and flow rate of air through the bubbler were obtained by regulating the pressure of the air supply and adjusting needle valves (NV) while reading a flow meter (FM) and pressure gauge (PG). Rates of water flow through roots and stems were measured by timing the rise of liquid in a pipette (P). Height of liquid in the pipette was adjusted between measurements with a screw-fed syringe (S). The solution was sampled or discarded through a ball valve (BV). The horizontal dashed lines (B) show the levels at which roots and stems were progressively cut for measurements of water flow after the measurements with attached roots were completed.

were immersed and care was taken to avoid any heating of stem tissues. Heat-treated plants were returned to nutrient solution in the controlled environment chamber where they wilted 3 days after treatment. Root and stem resistances were measured at various times after heating by the methods already described (Fig. 1-B).

Transpiration rate and leaf water potential.—Simultaneous and continuous measurements of transpiration rate and leaf water content were done on individual leaves in a leaf chamber. The leaf chamber was part of an open-ended system for leaf-gas exchange measurements and contained a beta gauge (5) for

measuring leaf water content. With the exception of a larger chamber volume and a dew point meter (Cambridge Systems® Model 880) to measure humidity, the leaf chamber was generally similar to the one used previously on tomato (4, 8). The leaf area was traced on paper and the leaf was installed in the chamber. The base

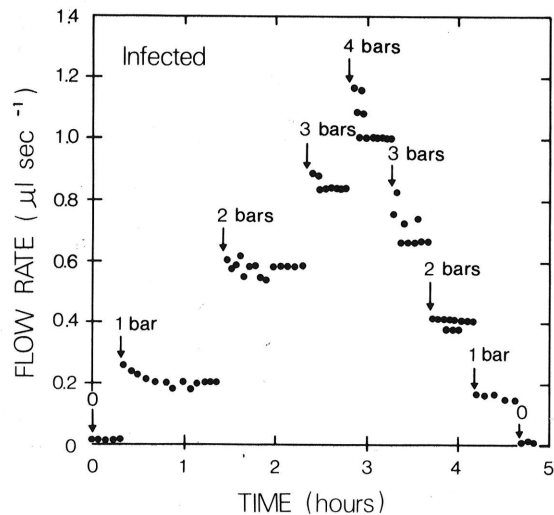
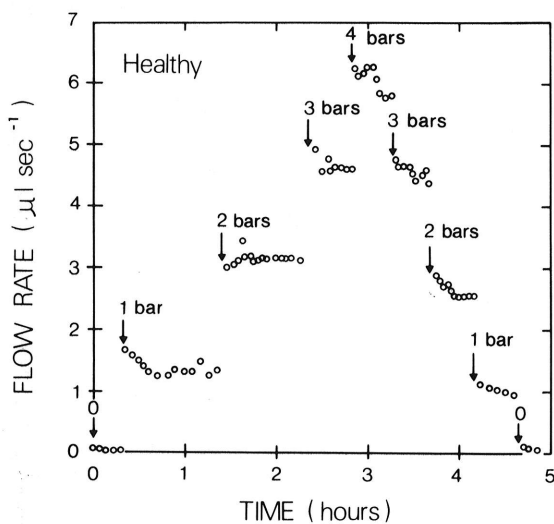


Fig. 2. Influence of progressive increases and decreases in pressure on rates of water flow through healthy and infected safflower roots on the third day after inoculation with *Phytophthora cryptogea*. Stems were cut at the cotyledons (Fig. 1-A) and one healthy and one infected plant were simultaneously used in the pressure apparatus. Pressure was changed to the values given above the arrows at the times indicated by the arrows.

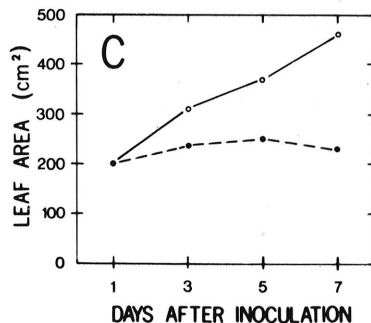
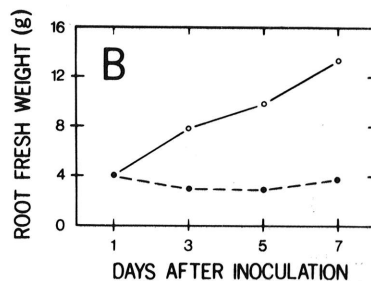
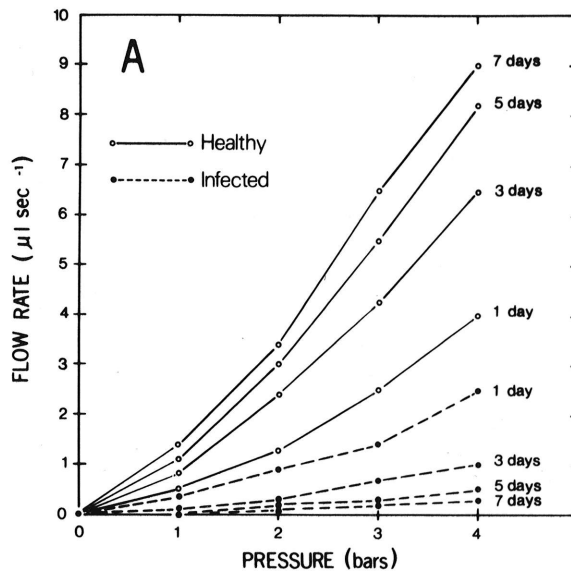


Fig. 3-(A to C). A comparison of healthy safflower plants with safflower plants infected with *Phytophthora cryptogea*: **A)** Rates of water flow through excised roots; **B)** root fresh weights; and **C)** leaf areas measured 1-7 days after inoculation. Rates of water flow (A) were measured by progressively increasing the pressure applied to roots cut from plants at the cotyledons (Fig. 1-A). Root fresh weights (B) and leaf areas (C) are the totals for the healthy (open circles) and infected plants (closed circles) used to obtain rates of water flow (A).

of the leaf was then cut from the stem under freshly boiled water and allowed to come to a steady-state transpiration rate and water content. Leaves required 1-6 hr to come to the steady state defined previously (4). Finally, the leaf was quickly removed from the chamber and placed directly in a thermocouple psychrometer (5) to determine its water potential (ψ). Although conditions in the leaf chamber were maintained as constant as was possible during measurements on any one leaf, light, temperature, and humidity were initially manipulated to give various steady-state transpiration rates. Quartz-iodine lamps provided $10\text{--}300\text{ W}\cdot\text{m}^{-2}$ of light in the 300- to 700-nm wave band. Leaf temperatures were between 20 and 35 C and the water vapor content of the ambient air was $3\text{--}20\ \mu\text{g}\cdot\text{cm}^{-3}$. Leaf chamber measurements were done on six healthy and five infected plants 4-6 days after inoculation.

Transpiration rates of intact plants were measured as the rates of weight loss by individual plants in solution culture during light periods in the controlled environment chamber. Periodically, during 3-4 hr periods when transpiration rates were found to be constant, all the leaves of representative plants were quickly cut and individually placed in thermocouple psychrometers to determine their ψ values. Leaf areas were determined at the conclusion of the transpiration measurements.

Calculations and units of resistance.—Resistance was calculated according to the transport equation:

$$R = \frac{\Delta\psi}{F}$$

where R is the resistance to liquid water flow, F is the rate of water flow, and $\Delta\psi$ is the total water potential difference (15). Rates of water flow due to transpiration are calculated on a leaf area basis in units of $\text{g}\cdot\text{cm}^{-2}\cdot\text{sec}^{-1}$ which can be reduced to $\text{cm}\cdot\text{sec}^{-1}$. The corresponding units of resistance are $\text{bars}\cdot\text{sec}\cdot\text{cm}^{-1}$. Even though water flow in roots and stems may not be functionally related to leaf area, leaf area generally was used to give units of $\text{bars}\cdot\text{sec}\cdot\text{cm}^{-1}$ for resistances of roots and stems. The resistances of the roots, stems, and leaves are in series and are additive (15). Therefore, use of the same units for all parts of the plant shows the impact of various component resistances on the water relations of the intact plant. When uncut roots were in the pressure apparatus, the average ψ_s values of xylem sap in healthy plants, xylem sap in infected plants, and the nutrient solution were -0.14 , -0.56 , and -0.61 bar, respectively. These ψ_s values together with the pressure were used to calculate the total ψ difference. Furthermore, resistances attributed to the roots and individual stem segments were obtained by subtracting resistances of the appropriate stem segments from the resistances actually measured in the pressure apparatus (Fig. 1-B).

RESULTS

Influence of infection on root and stem resistance.—The influence of progressive increases and decreases in pressure on water flow through roots is shown in Fig. 2. Rates of water flow through both healthy and infected roots became nearly constant shortly after the pressure was changed to a new constant value. Furthermore, ascending or descending changes in pressure of equal magnitude generally caused similar

changes in flow rate. In subsequent experiments, rates of water flow through healthy and infected roots were compared 10-30 min after the pressure was increased.

Representative data obtained by applying pressures of 1-4 bars to healthy and infected roots at various times after inoculation are shown in Fig. 3-A. On the first day (24 hr) after inoculation, when healthy and infected roots had the same fresh weight (Fig. 3-B), infection decreased the flow rates by about one-third. Both the fresh weights (Fig. 3-B) and flow rates (Fig. 3-A) of healthy roots

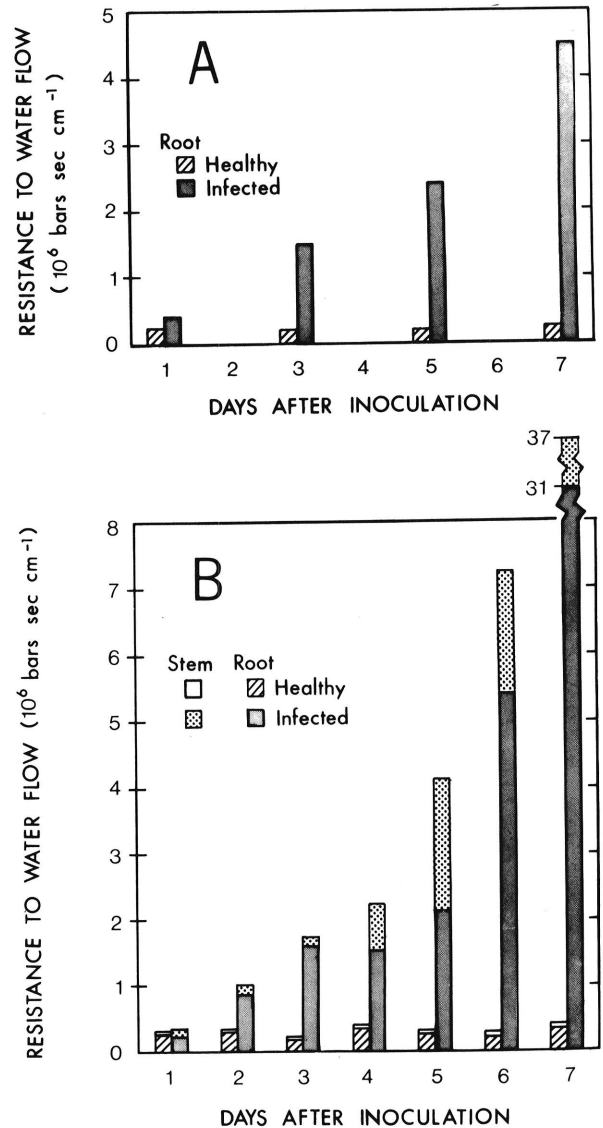


Fig. 4-(A and B). Influence of infection of safflower by *Phytophthora cryptogea* on root and stem resistances to water flow. A) Resistances of roots excised at the cotyledons (Fig. 1-A) calculated from the data in Fig. 3. B) Resistances of roots and stems observed when stems were initially cut for the pressure apparatus at the second pair of adult leaves (Fig. 1-B). Resistances were calculated by expressing flow rates on a leaf area basis.

increased more than twofold between 1 and 7 days after inoculation. In contrast, infected roots did not increase in fresh weight (Fig. 3-B) and had progressively lower flow rates (Fig. 3-A) as disease developed between 1 and 7 days after inoculation.

In all of the experiments of the type shown in Fig. 3-A, higher pressures had a disproportionate influence on water flow through roots; i.e., the lines relating flow rate to increasing pressure curved upward. Pressure-flow relationships for healthy roots generally are not linear and Fiscus (9) discusses the nonlinear nature of pressure-induced water flow through healthy roots. The flow rates obtained with healthy safflower roots at 2 bars pressure (Fig. 3-A) were similar to the transpiration rates of intact healthy plants and, therefore, were used to calculate root resistance.

Resistance to water flow through infected roots, as calculated on a leaf area basis, increased greatly with time after inoculation in contrast to the resistance of healthy roots which remained nearly constant (Fig. 4). Infection also increased the resistance of the lower stem 4-7 days after inoculation (Fig. 4-B). The first visible wilting of leaves on infected plants occurred 5 days after inoculation when the resistances of infected roots and stems were more than 8 and 40 times the respective resistances in healthy plants.

Infection greatly increased xylem resistance in both the uppermost roots and lower stems (Table 1). The increases in xylem resistance extended up the stem into internodes from which *P. cryptogea* was not isolated (Table 1). In one experiment, the radii of vessels in stem segments were used in Poiseuille's law to predict resistances to water flow (3). A comparison of resistances observed with the pressure apparatus with those predicted for the same segments by Poiseuille's law (Table 2) shows that only a small portion of the increase in xylem resistance in infected plants is due to decreases in the dimensions of the xylem.

Influence of heating roots on root and stem resistance.—Although heating roots initially decreased their resistance, Fig. 5 shows that the resistances of roots

and stems increased with time after noninoculated roots were heated. By the 3rd day after treatment the heated plants were wilted and their root and stem resistances (Fig. 5) were as large as those associated with wilting in infected plants (Fig. 4).

Influence of infection on resistance to movement of liquid water in leaves.—Resistances calculated from leaf chamber measurements of transpiration and ψ on leaves from healthy and infected plants, respectively, averaged 2.70×10^5 and 2.65×10^5 bars·sec·cm⁻¹. All the leaves in both treatments had resistances within a range of 2.18×10^5 to 3.36×10^5 bars·sec·cm⁻¹. There was no consistent variation in leaf resistance with variation in leaf ψ between -3.6 and -7.3 bars during the measurements or with time after inoculation.

Influence of infection on transpiration rate and leaf water potential in intact plants.—Transpiration rates and ψ values obtained with representative healthy and infected plants under the conditions used for plant growth were used to calculate total resistances to water flow for intact plants (Table 3). Resistances calculated for the intact plants are nearly equivalent to the sums of the resistances obtained with the appropriate plant parts (Table 3).

TABLE 2. Resistances to water flow observed in the pressure apparatus and predicted by Poiseuille's law for stem segments from healthy safflower plants and safflower plants infected with *Phytophthora cryptogea*^a

Days after inoculation	Plant	Resistance to water flow (bars·sec·cm ⁻³) ^b	
		Observed	Predicted
5	Healthy	31	12
	Infected	920	14
6	Healthy	13	5
	Infected	1,530	11

^aRepresentative data for stem segments from the third internode above the roots of three plants (Fig. 1-B).

^bCalculated on the basis of flow rate (cm³·sec⁻¹).

TABLE 1. Resistances to water flow and isolations of *Phytophthora cryptogea* obtained with root and stem segments from healthy and infected safflower plants^a

Days after inoculation	Plant segment	Resistance to water flow (bars·sec·cm ⁻³) ^b		Isolation of <i>P. cryptogea</i> (%) ^c	
		Healthy	Infected	Healthy	Infected
3	Root ^d	10	310	0	100
	Internode 1 ^e	12	180	0	50
	Internode 2	29	130	0	0
	Internode 3	15	80	0	0
5	Root ^d	20	4,450	0	94
	Internode 1 ^e	15	1,220	0	78
	Internode 2	26	980	0	45
	Internode 3	24	650	0	0

^aRepresentative data for four replicate plants.

^bCalculated on the basis of flow rate (cm³·sec⁻¹).

^cPercentage of 15-30 cross sections yielding growth of *P. cryptogea* on selective medium.

^dCalculated for the upper 3 cm of roots remaining after roots were cut under water (Fig. 1-B).

^eStem internodes are numbered from the roots up (Fig. 1-B).

DISCUSSION

The total resistances reported here for healthy safflower are within the range of values reported for other herbaceous species (1, 10, 14, 16). In addition, the resistances obtained for the excised parts of safflower are reasonably close to some of the values reported in the literature for roots (2, 11), stems (1, 3, 4, 11), and leaves (2). In healthy safflower, 44, 13, and 43% of the total resistance can be attributed to the roots, stems, and leaves, respectively. Evidently, leaves account for a larger fraction and roots a lesser fraction of the total resistance in safflower than do the leaves and roots of some other species (1, 14, 15).

During the development of *Phytophthora* root rot in safflower, resistances to water flow through the roots and stems progressively increase and, under the conditions used, finally become large enough (Fig. 4) to depress leaf ψ (Table 3) to values where leaf wilting occurs (5). There is

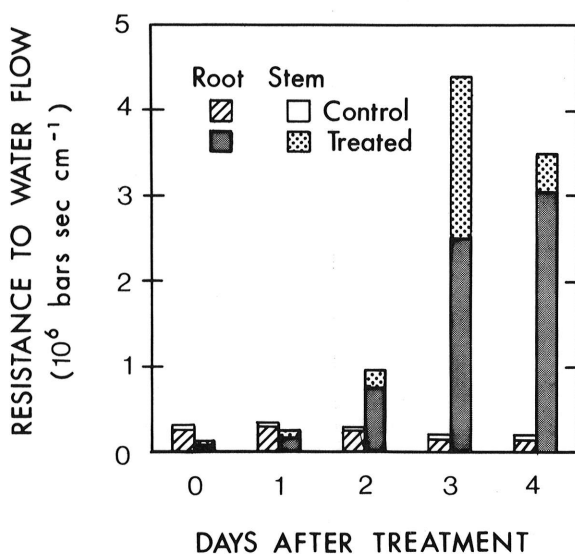


Fig. 5. Influence of heating safflower roots on root and stem resistances water flow. Stems were initially cut for the pressure apparatus at the second pair of adult leaves (Fig. 1-B) and resistances were calculated by expressing flow rates on a leaf area basis.

no change in the transpirational behavior of safflower infected with *P. cryptogea* that contributes to the development of water stress (5), and the quantitative estimates of resistance presented here confirm earlier suggestions (5) that increased resistance to water uptake within infected plants is the sole cause of the wilt symptoms.

Although the transpirational demand and ψ_s vs. ψ relationships of plant cells can alter the influence of resistance to water uptake on turgor, the results presented here indicate that resistance to water flow within infected plants must become very large before the resistance alone can cause lasting wilt symptoms in plants that are well supplied with water at the roots. Infected plants did not wilt 4 days after inoculation, even though their total resistance was four times that of healthy plants (Fig. 4-B). When the first wilting occurred 5 days after inoculation, the total resistance of infected plants was five to seven times that of healthy plants, and by the time leaves were severely wilted, the resistance of infected plants was more than 40 times the healthy value (Table 3). Fivefold or greater increases in total plant resistance have previously been associated with wilting due to *Fusarium* wilt in tomato (4) and *Aphanomyces* root rot in sugar beet (16). Stomatal closure at low ψ values in leaves of safflower affected by *P. cryptogea* (5) reduces transpirational flow and, therefore, tends to prevent large depressions of leaf ψ when resistance to water uptake increases. The data in Table 3 illustrate the compensating type of interactions that occur between transpiration rate, leaf ψ , and total resistance to water movement in infected safflower. Even though very large increases in resistance are evidently required for lasting wilt symptoms to develop, it should be noted that all measureable increases in resistance to water uptake caused by infection (Fig. 4) are potentially damaging to the water relations and physiology of the host. The impact of increased resistance to water uptake within the plant will increase with evaporative demand and with depletion of soil water to an extent that additional resistances to plant water uptake in the soil become significant (15).

As infected safflower plants began to wilt, nearly half the resistance to water flow through infected plants was located in the xylem of the upper roots and lower stem (Fig. 4-B). The greatest increases in xylem resistance occurred in those root and stem segments in which the xylem contained mycelium and other foreign material

TABLE 3. Transpiration rates, leaf water potentials, and total resistances to liquid water flow of healthy safflower plants and safflower plants infected with *Phytophthora cryptogea*

Plant	Days after inoculation	Condition of the leaves	Measurements on intact plants ^a		Total plant resistance (10 ⁶ bars · sec · cm ⁻¹)	
			Transpiration rate (μg · cm ⁻² · sec ⁻¹)	Leaf water potential ^b (bars)	Measurements on intact plants ^c	Measurements on excised plant parts ^d
Healthy	5	All turgid	5.2	-4.5	0.78	0.62
Infected	5	Some wilted	2.3	-9.4	3.8	4.4
Infected	7	All wilted	0.4	-14.3	34.2	37.2

^aRepresentative data for three replicate plants.

^bAverage ψ value for all leaves on one plant with roots in nutrient solution at $\psi_s = -0.6$ bars.

^cCalculated from the transpiration rate and average ψ value of leaves on intact plants.

^dResistance of excised roots and stems (Fig. 4-B) plus the resistance of excised leaves.

and from which *P. cryptogea* was readily isolated. However, increases in xylem resistance extended at least one or two internodes above the highest point of stem invasion by the pathogen (Table 1) and at least 4-10 cm above the highest point where foreign material was observed in the xylem. Of course, there may have been intermittent plugging of the xylem which was not observed in the cross sections of the upper stem.

Observations that infection of safflower by *P. cryptogea* increases xylem resistance in noninvaded regions of the stem suggest the involvement of toxins that alter xylem function. More than 20 years ago Wolf and Wolf (18) and Schramm and Wolf (17) suggested *P. parasitica* var. *nicotianae* produces a toxin that increases xylem resistance. *Phytophthora cryptogea* may also synthesize a toxin that alters xylem function, but the resistances to water flow which develop 2-4 days after noninoculated roots are heated (Fig. 5) suggest increased xylem resistance in infected safflower may be a more indirect result of root damage. The experiments were not done aseptically and saprophytic microorganisms may have contributed to the influence of heat treatment on resistance to water transport. Similarly with Phytophthora root rot, secondary organisms may influence the physiology of infected safflower plants both in the laboratory and in the field. In any case, in the absence of a known pathogen, dead or dying roots evidently can release substances that move up the stem and impair xylem function, and it is possible that the same or similar substances are released from roots decayed by *P. cryptogea*. The results presented here and elsewhere (5) clearly show that wilt-inducing toxins of a type that act on leaf cells rather than resistance to water uptake (12) are not involved in the wilting of safflower plants infected with *P. cryptogea*.

The differences in resistance to water flow through healthy and infected safflower roots always were much larger than the differences in the size of root systems (Fig. 3 and 4). Reductions in root surface area, therefore, can only account for a fraction of the resistance induced by infection. Although infection also may increase resistance to radial water flow from the root surface to the xylem, a resistance that was not measured separately, measurements of longitudinal water flow through root segments (Table 1) suggest a large part of the resistance of infected roots (Fig. 4) can be attributed to the xylem.

The influence of infection by *P. cryptogea* on the physiology of safflower obviously exceeds visual estimates of the damage to roots. In fact, resistance to water transport within the host becomes so large during disease development that reduced root density and distribution in the soil are only likely to be of secondary importance to the water relations of safflower infected with *P. cryptogea*. With the possible exception of Phytophthora root rot in tobacco (17, 18) and Aphanomyces root rot in sugar beet (16), which also appear to increase plant resistance to water transport, the influences of other root rots on water flow within the plant and the availability of soil water to the plant remain unknown. Large resistances at least can be suspected to occur within plants when root diseases cause them to wilt in relatively wet soil under mild transpirational conditions.

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