

Transient Changes in Hydraulic Resistance Caused in Corn Roots by *Fusarium moniliforme*

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ABSTRACT

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Analysis with a water transport model of the diurnal cycles of diffusive resistance and water potential of field-grown corn plants indicated that plants infected nonsystemically with *Fusarium moniliforme* following predisposition by an early-season water stress had transient increases in whole-plant hydraulic resistance. Similarly infected plants grown under steady-state conditions in growth chambers at relatively low vapor pressure deficits (VPD) (low transpirational flux) had significantly higher and constant resistance compared to noninfected and infected plants that had

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not been predisposed by a water stress. However, infected predisposed plants grown under conditions of higher VPDs (higher transpirational flux) showed the same cycling of resistance as was observed in the field. These results indicate that the source of increased resistance dissipated as a function of water flow through the plant. The site of increased resistance was in the roots rather than the stem. Diurnal vascular gel deposition in response to infection is implicated as the source of variable resistance.

In a previous investigation (17) plant and soil water relations were described for corn (*Zea mays* L.) as affected by nonsystemic root infection by *Fusarium moniliforme* (Sheld.) emend. Snyd. & Hans., a causal agent of stalk rot of corn. Analyses of several plant and soil parameters indirectly indicated that increased resistance to liquid water flow (hydraulic resistance), rather than an alteration in stomatal functioning, was responsible for the abnormal water relations that caused the plant to behave as if it was chronically stressed by a water deficit. However, because the study was conducted under dynamic meteorological conditions in the field, the magnitude, duration, and location of the altered hydraulic resistance could not be determined with certainty.

The present paper describes the use of a water transport model and a series of steady-state experiments to quantitatively assess the altered hydraulic resistance in corn plants infected with *F. moniliforme*.

MATERIALS AND METHODS

The water transport model. Plant water relations data from the previous study (17) were evaluated with the model proposed by Elfving et al (9) and Kaufman and Hall (11) which is based on the soil-plant-atmosphere continuum theory of water transport first described by van den Honert (18). This theory states that

$$\text{Flux} = (\psi_{\text{soil}} - \psi_{\text{root}}) / r_{(\text{soil to root})} = (\psi_{\text{root}} - \psi_{\text{leaf}}) / r_{(\text{root to leaf})} = \text{VPD} / r_{(\text{leaf to air})}$$

in which ψ is water potential, r is flow resistance, and VPD is vapor pressure deficit, ie, the difference in absolute humidity between leaf and air. Thus, if $r_{(\text{leaf to air})}$, leaf temperature, relative humidity, and air temperature are known, flux can be estimated as VPD divided by the leaf-to-air diffusive resistance (the units are: mm Hg·cm⁻¹·sec⁻¹) (11). In this study, it was assumed that the air spaces in the leaves were at saturation vapor pressure at leaf temperature, which was measured with a thermal infrared remote sensing thermometer (Raytek Instruments, model Raynger II,

Mountain View, CA). Air temperature and humidity were measured with a sling psychrometer and vapor pressure was derived from appropriate tables (6). Measurements of $r_{(\text{leaf to air})}$ and ψ_{leaf} were made with a diffusion porometer and pressure chamber apparatus, respectively, as described previously (17). This means of estimating transpirational flux was verified with plants grown under constant environmental conditions as described in the next section.

Flux estimates for the field-grown plants (17) were calculated for previously stressed and nonstressed plants 3 days after an irrigation while the soil was at field capacity and while ψ_{plant} was declining until early afternoon. Plants were stressed by withholding an irrigation until the midday ψ_{leaf} was at least 2 bars lower than the adequately watered controls. By graphically relating flux estimates with ψ_{plant} , it is possible to distinguish major differences among plants in $r_{(\text{soil to leaf})}$ even though steady-state conditions did not prevail.

Growth chamber experiments. Hydraulic resistance was determined under steady-state conditions of evaporative demand for previously water-stressed and nonstressed plants grown in infested and noninfested soil. Corn plants (Hybrid SX98, P-A-G Seeds, Minneapolis, MN 55402) were grown in pots containing 4.4 L of soil either noninfested or infested with ground barley straw inoculum of *F. moniliforme* (0.5 g inoculum per kilogram of soil) (17). Several seeds were planted in each pot so that seedlings could be thinned to uniform size (one per pot) 1 wk after emergence. Plants were grown in a greenhouse at 22 C and irrigated with half-strength Hoagland's solution twice weekly for 4 wk, then water was withheld from the two stressed treatments until the midday ψ_{leaf} was about 3 bars lower than the nonstressed treatments. After recovery from water stress, all plants were watered identically and maintained for an additional week in the greenhouse before being moved into the growth chambers. Growth chambers were maintained at 20.0, 25.5, 29.4, and 35.1 C (± 0.2 C) with relative humidities of 54, 51, 42, and 44% ($\pm 2\%$), respectively, which gave VPDs of 8.32, 11.99, 17.83, and 23.62 mm Hg, respectively. Incandescent and fluorescent light bulbs provided photosynthetically active radiation of 800 microeinsteins·m⁻²·sec⁻¹ (40,000 lux), about 40% of full sunlight. Two oscillating fans were installed in each chamber to eliminate VPD gradients and to minimize the boundary layer resistance to vapor diffusion from leaf surfaces.

Eight plants from each treatment were placed in each chamber 2 days prior to the day on which measurements were made. The night before the test day, pots were watered, allowed to drain briefly, and

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then placed in polyethylene bags the openings of which were sealed to the base of the stalks. The plants and pots were weighed 1 hr before the lights came on, 1 hr after the lights came on, and at about 2-hr intervals thereafter. Determinations of ψ_{leaf} , r_{leaf} , and leaf surface temperature were made as previously described. When soil and plant weight decreased by more than 100 g, a known amount of water was added to the soil through a vapor-tight port in the bag. Two plants stripped of leaves but sealed in polyethylene bags were included in each chamber and weighed periodically to account for transpiration through the stem surface. Immediately after the last determinations during the day, leaves from each of six plants from each treatment were removed and photocopied. The photocopied images were cut out, weighed, and leaf area calculated by reference to photocopies of known area. Tissue samples from the first internode of each plant were surface-sterilized in 0.26% sodium hypochlorite, rinsed in sterile water, and plated on potato-dextrose agar to determine if *F. moniliforme* was present. Several soil cores of known volume were removed from each pot for determinations of total root length per plant and infections per 100 cm root as previously described (17). Mean root diameter was 274 μm . Roots that coiled at the bottom of the pots accounted for less than 5% of total root length and were not included in the final measurements or calculations. Experiments were repeated twice with similar results.

A separate experiment was conducted to evaluate the method of estimating transpirational flux as used for field-grown plants. Plants were grown in noninfested soil as described above but were not water-stressed. They were then exposed to regimes that resulted in the same VPDs as described above. In addition, the experiment was repeated except that light intensity was reduced to 350 $\mu\text{mol photons m}^{-2}\text{sec}^{-1}$. This resulted in higher $r_{(leaf\ to\ air)}$ hence lower rates of transpiration. Thus, there were eight treatments that permitted a statistical correlation between estimated and actual transpirational flux.

Resistance to water flow. Hydraulic resistance was calculated according to a transposition of the equation given above such that

$$r_{(soil\ to\ leaf)} = (\psi_{soil} - \psi_{leaf}) / \text{Flux}$$

in which flux is expressed as cubic centimeters of water per centimeter of root length per hour per bar. During the experiments, ψ_{soil} did not fall below -0.15 bars as determined from a moisture release curve (*unpublished*). Resistance to flow in the xylem between roots and leaves of healthy plants accounts for a small proportion of whole-plant resistance (12,14,15), and hydraulic resistance in saturated soil is negligible (5,10,16).

An additional experiment was conducted to determine if the primary site of hydraulic resistance was in the roots or shoots. Three plants per treatment were prepared as previously described and grown at 35.1 C. At 1 hr after the lights came on, ψ_{leaf} was determined, the bagged pots were immersed in degassed water up to the first node, and the stem was cut at the first internode. Leaf ψ was then determined at about 15-min intervals for 1 hr under growth chamber conditions.

RESULTS

Analysis of the water relations of the field-grown plants by the water transport model of Elfving et al (9) and Kaufman and Hall (11) indicated that there were drastic differences in hydraulic resistance between the stressed-infested and the other three treatments (Fig. 1). The steep decline followed by a sudden increase in ψ_{leaf} as transpirational demand increased is unprecedented in the water relations literature of healthy or diseased plants and suggests that an initially high resistance in the stressed-infested treatment decreased markedly as transpirational flow increased. Leaf ψ in the other three treatments steadily declined with increasing transpirational demand (Fig. 1), confirming reports by others (1,11,14) for corn and other plants grown under similar conditions. The high correlation ($R^2 = 0.97$) between actual transpirational flux and VPD/r_{leaf} (Fig. 2) determined under steady state

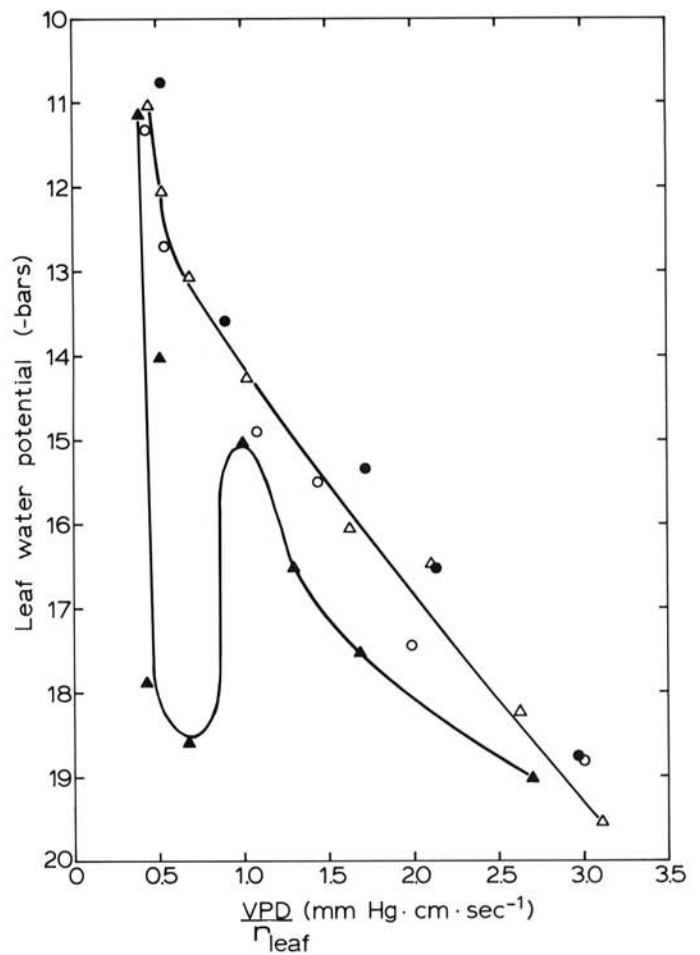


Fig. 1. Relationships between leaf water potential and transpirational flux as estimated by the ratio of vapor pressure deficit (VPD) to leaf diffusive resistance (r) for field-grown corn plants in soil either noninfested or infested with *Fusarium moniliforme* and either exposed to a mild early-season water stress or nonstressed as follows: Noninfested, nonstressed (O—O); noninfested, stressed (●—●); infested, nonstressed (Δ — Δ); and infested, stressed (\blacktriangle — \blacktriangle). Each point represents the mean of five determinations. Mean standard error over all treatments is 2.1 bars.

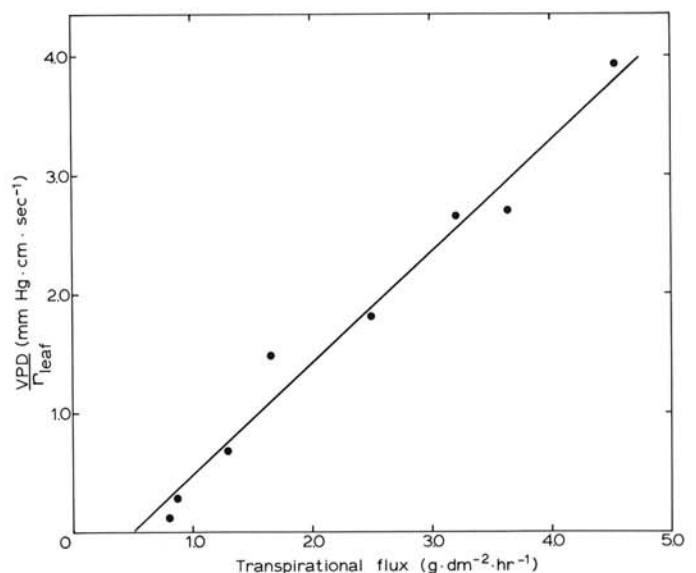


Fig. 2. Relationship between estimated (VPD) and actual transpirational flux (TF) for corn plants as determined under steady-state conditions. The regression equation is $TF = 1.081 (VPD) + 0.502$, $R^2 = 0.97$.

conditions suggests that this method for estimating transpirational flux is valid.

At a VPD of 20.0 mm Hg, hydraulic resistance of the stressed-infested plants was about 50% higher than the other three treatments throughout the 8-hr period of measurement (Fig. 3A). At 25.5 mm Hg, the relationships among resistance in the four treatments were equivalent to those at 20.0 mm Hg during the first hour after the lights came on, but then resistance in the stressed-infested treatment decreased linearly until there was about a 25% difference in resistance between it and the other three treatments at 7 hr (Fig. 3B). At 29.4 mm Hg, resistance in the stressed-infested treatment was about two-fold greater than the other three for the first 6 hr but then fell abruptly such that there were no significant differences among the four treatments by 7 hr (Fig. 3C). At 35.1 mm Hg VPD, resistance for the stressed-infested treatment was more than two-fold larger than that of the other three treatments 1 hr after the lights came on (Fig. 3D); it then declined and by 5.5 hr was the same as the other treatments. Resistances reported in this study for uninoculated and nonstressed plants in growth chambers are similar in magnitude to those reported for other herbaceous plants (5,7,16).

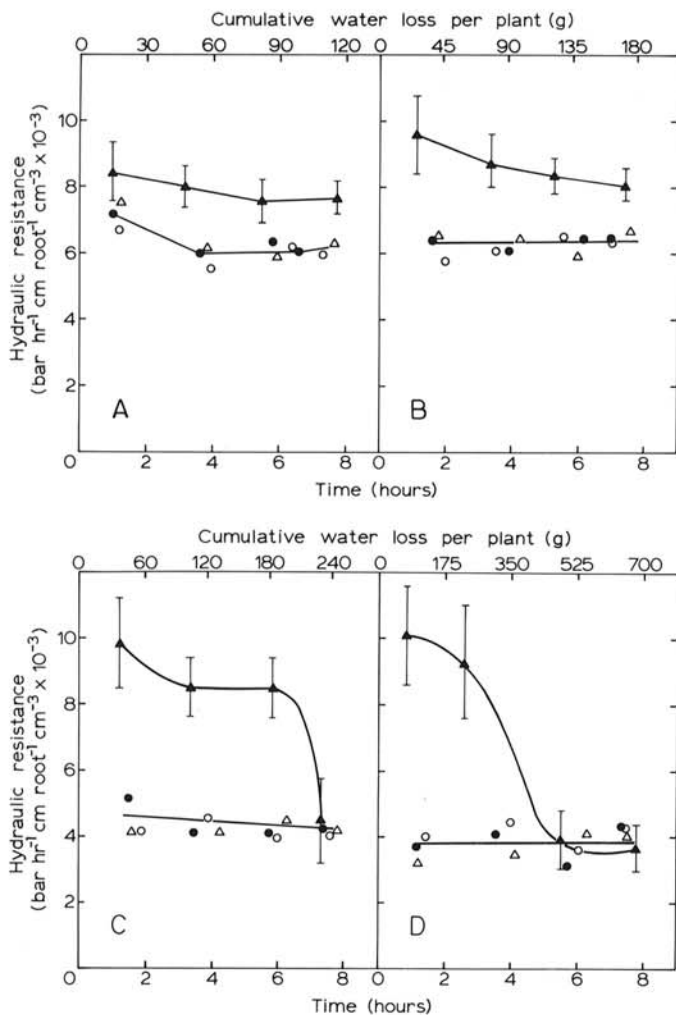


Fig. 3. Relationships between hydraulic resistance and time after the onset of steady-state evaporative demand conditions for corn plants grown in soil either noninfested or infested with *Fusarium moniliforme* and either previously exposed to a mild water stress or nonstressed as follows: Noninfested, nonstressed (○—○); noninfested, stressed (●—●); infested, nonstressed (△—△); infested, stressed (▲—▲). Values for cumulative transpirational water loss per plant for the infested-stressed treatment appear on the upper abscissa. During the period of observation, plants were maintained at vapor pressure deficits of A, 8.32; B, 11.99; C, 17.83; and D, 23.62 mm Hg. Each point represents the mean of eight determinations. Vertical bars indicate the standard error for the infested, stressed treatment.

The roots from plants in the growth chambers did not show any symptoms of infection nor was *F. moniliforme* recovered from any stem tissues. However, rates of root infection in the stressed and nonstressed infested treatments were 63 and 11 colonies per 100 cm of root length, respectively.

Cumulative water loss for the stressed-infested treatment is included in Fig. 3A to D. Values on the upper abscissa indicate the amount of water transpired at the time indicated on the lower abscissa. Water loss as a function of time was statistically linear for all four VPDs, and the regression equations were calculated for presentation in Fig. 3. At the two higher VPDs, the sudden changes in resistance occurred after about 180 g of water per plant had been lost by transpiration (Fig. 3C and D), while at the two lower VPDs, cumulative transpirational loss did not exceed 180 g (Fig. 3A and B). Rates of water loss for the other three treatments were nearly identical to that of stressed-infested treatment indicating that transpirational flux was maintained at the expense of ψ_{leaf} (see second equation).

Rates of ψ_{leaf} recovery for the first 15 min following excision of the stems under water for the stressed, infested and the other three treatments were 0.44 and 0.33 bars/min, respectively (Fig. 4). Recovery rates were essentially identical in all four treatments for the duration of the hour.

DISCUSSION

Analysis of the water relations of the field-grown plants by the water transport model of Elfving et al (9) and Kaufman and Hall (11) indicated that there was a variable resistance to water flow in the previously stressed, infested plants. The steep decline and sudden increase in ψ_{leaf} as VPD increased seems to have been caused by a diurnal deposition and removal of an obstruction to water flow in the plant. While data from only 1 day are presented (when soil moisture was at field capacity), analysis of the data presented previously (17) indicated that this pattern occurred daily. Calculations of resistance for the growth chamber experiments confirmed the occurrence of the transient increase in resistance to water flow in the stressed-inoculated treatment observed under field conditions.

Because there were no differences in stem resistance among treatments, it is concluded that the primary site of altered hydraulic resistance was in the roots. In contrast, Duniway (8) showed that hydraulic resistance in roots and stems of safflower infested with *Phytophthora cryptogea* increased irreversibly during disease

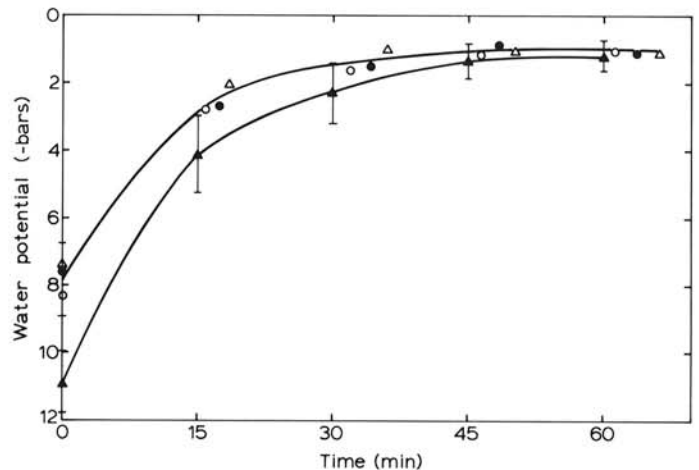


Fig. 4. Relationships between plant water potential and time after severing immersed stems of corn plants grown in soil either infested with *Fusarium moniliforme* or noninfested and either previously exposed to a mild water stress or nonstressed as follows: Noninfested, nonstressed (○—○); noninfested, stressed (●—●); infested, nonstressed (△—△); and infested, stressed (▲—▲). Each point represents the mean of three determinations. Vertical bars indicate the standard error for the infested-stressed treatment.

development and did not decrease with water flow. In the present study, the steep declines in root resistance occurred after about 180 g water had been transpired. Based on the mean root diameter and total root length measured in this study and the volumes of corn root xylem reported by Miller (13), a flux of 180 g of water would require that the root xylem transport about 80 times its volume in water.

The sudden decrease in apparent root resistance and the large volume of water transpired before the effect was observed, suggest that an obstruction to water flow was either reduced in a manner that is dependent upon water flux or was swept into xylem elements with extremely large diameters within a short time. Spores and other foreign material are known to be deposited and carried in the transpirational stream and have been implicated in obstructing water flow (2,3). However, it seems improbable that such a mechanism could account for the phenomenon reported here because it would be unlikely that all of the obstructions would be dislodged simultaneously. Furthermore, *F. moniliforme* was not recovered from the first internode, roots were not systemically infected, and there were no differences in stem resistance among treatments. However, the lack of differences among treatments in leaf internal water relations suggests that there was a transient physical obstruction to water flow rather than a disruption in membrane permeability as might be caused by a translocatable toxin (2,8,17). At the time infected plants were used in this study they had no obvious symptoms of infection or water stress.

The studies of Beckman (4) and VanderMolen et al (19) provide a plausible explanation for the transient increases in root resistance reported here. They showed that vascular gel formation in a variety of plants is a general response to infection by vascular parasites. Furthermore, they provided evidence that vascular gels, which partially occlude xylem elements, swell and shrink in diurnal cycles; the entire process being dependent on water flux. Interestingly, Duniway (7) reported that the increase in hydraulic resistance of tomato infected with *F. oxysporum* was not associated with the root system through which infection had occurred, but rather with the stem. However, in attempting to measure resistance in detached stems with a pressure-flow apparatus, he reported that resistance declined as a function of water flow through the stem and that there was no foreign material or increase in viscosity in the exuded water. Attempts to measure hydraulic conductivity in the roots and lower stems of corn plants in such an apparatus were unsuccessful because of the high rate of air infusion through the brace roots.

Regardless of the mechanism by which hydraulic resistance is affected, the lasting effects on the plant are significant. Diurnal cycles of water stress caused by increased root resistance result in altered assimilate partitioning in corn. This eventually leads to root senescence and enhanced susceptibility to stalk rotting pathogens (17).

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