

Increases in Water Potential Gradient Reduce Xylem Conductivity in Whole Plants. Evidence from a Low-Pressure Conductivity Method¹

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A new method using hydrostatic suction (less than 0.02 MPa) was used to measure whole-root conductivity (K_r) in saplings of two angiosperm pioneer trees (*Eucalyptus regnans* and *Toona australis*) and two rainforest conifers (*Dacrycarpus dacrydioides* and *Nageia fleurii*). The resultant K_r was combined with measurements of stem and leaf hydraulic conductivity to calculate whole-plant conductivity and to predict leaf water potential (Ψ_1) during transpiration. At normal soil temperatures there was good agreement between measured and predicted Ψ_1 during transpiration in all species. Changes in the soil-to-leaf water potential gradient were produced by root chilling, and in three of the four species, changes in Ψ_1 corresponded to those expected by the effect of increased water viscosity on K_r . In one species, however, root chilling produced severe plant wilting and a decline in Ψ_1 significantly below the predicted value. In this species Ψ_1 decreased to a value close to, or below, the Ψ_1 at 50% xylem cavitation. It is concluded that decreased whole-plant conductivity in *T. australis* resulted from a decrease in xylem conductivity due to stress-induced cavitation.

At least one-half of the resistance to hydraulic flow through plant vascular systems occurs in the root. The largest of these resistances occurs in the radial pathway through the root as water crosses from the root surface, through the cortex, to the vascular tissue (Steudle and Peterson, 1998). Under non-stressed conditions the resistance of the axial pathway from root xylem to the leaves represents only a small fraction of the total resistance of the plant (Kramer, 1938; Frensch and Steudle, 1989; Tsuda and Tyree, 1997). However, studies of axial hydraulic flow through roots and stems have shown that the conductivity of the xylem is dynamic and that embolisms caused by cavitations in xylem conduits can result in very large reductions in axial conductivity, particularly under conditions of water stress (for review, see Tyree and Ewers, 1991).

Xylem embolism increases as a sigmoidal function of xylem water potential (or applied air pressure) (Pammenter and Vander Willigen, 1998), resulting in a rapid loss of conductivity as water potential decreases below a critical level. Although typically associated with water stress, varying degrees of xylem embolism have been observed in virtually all studies of field-grown plants, regardless of stress exposure (Hargrave et al., 1994; Kolb and Davis, 1994; Alder et al., 1996), suggesting that in the field plants frequently operate at water potentials low enough to

initiate xylem cavitation. Clearly, cavitation of a large proportion of the functional xylem between the roots and leaves has the potential to shift the major hydraulic resistance in the plant from the radial pathway in the root to axial pathways in the root, stem, and leaves. This leads to an interaction between the vulnerability of the xylem to cavitation, the conductivity of the root, and the evaporative demand of the leaves. In seedling and sapling plants this interaction is particularly important, because competition for light and space often leads to increased carbon allocation to shoots and leaves at the expense of root tissue.

Two of the best correlates with seedling and sapling growth rates are leaf area ratio and leaf mass ratio (Walters and Reich, 1999), illustrating that root investment is commonly sacrificed to enhance growth rate during regeneration. As a result of this relative reduction in root investment, fast-growing pioneer species are often susceptible to water supply deficit. This is commonly observed in nature as wilting of pioneer species when exposed to high-light conditions or vapor-pressure deficit even when soil water is plentiful (Schultz and Matthews, 1997). Thus, there is a significant trade-off between the gains in carbon balance achieved by reducing root investment and the costs associated with either producing xylem and leaf tissue capable of resisting low water potential or suffering tissue damage during periods of high evaporative demand.

In this study we examined water flow through two fast-growing early pioneer species expected to be vulnerable to xylem cavitation and two rainforest conifers expected to be more resistant, under condi-

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tions of high evaporative demand, to determine the relative importance of xylem cavitation *in vivo*. This was achieved by measuring whole-plant hydraulic conductivity during imposed changes in the root-leaf water potential gradient. Rapid changes in the water potential gradients through experimental plants were made by chilling the roots of potted plants while transpiration rates were at a maximum. Hydraulic flow through roots has been shown to respond to temperature as an approximately linear function of the viscosity of water (Kramer, 1940; Hertel and Steudle, 1997), and these changes are large enough to have a profound effect on the hydraulic flux through tissues, e.g. changes in the viscosity of water between 25°C and 5°C will result in root conductance being reduced by about 40%. This enabled root conductance and root-stem water potential difference to be manipulated without the complicated effects of changing soil water potential.

Two methods were used to measure the hydraulic resistance of plant tissues, the evaporative flux (EF) technique and a hydrostatic pressure technique. The EF method involves measuring leaf water potential (Ψ_l) during periods of steady-state EF to calculate the hydraulic conductivity of the whole plant, whereas the hydrostatic pressure technique determines conductivity by measuring flow through excised tissue when a hydrostatic pressure differential (ΔP) is applied (Brouwer, 1954; Sperry et al., 1988).

The hydraulic conductivity of roots was measured using a modification of traditional pressure-induced flow techniques. With this method a low-pressure hydrostatic suction was applied to the stump of a plant that had been detopped under water. The kinetic response of hydraulic fluxes to two different suction pressures (-0.009 and -0.0175 MPa) were measured as was the hydraulic flux produced when $\Delta P = 0$. Root conductivity was calculated from the difference between flow during suction and passive flow at $\Delta P = 0$ (root pressure). We have assumed that Equation 1 is a good representation of water flow through the root:

$$Q = (\Delta P - \sigma\Delta\pi)/R \quad (1)$$

where Q is the hydraulic flux through the root, ΔP is the hydrostatic driving force, σ is the effective reflection coefficient of the whole root, $\Delta\pi$ is the change in osmotic pressure across the root, and R is the whole-root resistance.

Under hydrostatic tension the hydraulic flux through the root can be expressed by Equation 2:

$$J_t = L_p(\Delta P - \sigma\Delta\pi_t) \quad (2)$$

where J_t is the hydraulic flux under the tension ΔP (kilograms per second), L_p is whole-root conductivity (kilograms per second per megapascal), and $\Delta\pi_t$ is the change in osmotic pressure across the root under the tension ΔP .

Hence, when $\Delta P = 0$, the hydraulic flux will be expressed by Equation 3:

$$J_o = L_p\sigma\Delta\pi_o \quad (3)$$

where J_o is the hydraulic flux when $\Delta P = 0$, and $\Delta\pi_o$ is the change in osmotic pressure across the root when $\Delta P = 0$.

During rapid measurements of hydraulic flux under tension followed by hydraulic flux when $\Delta P = 0$, $\sigma\Delta\pi$ should change in proportion to the hydraulic flux, if it is assumed that the active transfer of solutes into the vascular stele remains unchanged between rapid measurements of exudation and hydrostatic flow and the effects of solvent drag are minimized by maintaining a low soil osmotic potential. Under these conditions the ratio of $\sigma\Delta\pi_o$ to $\sigma\Delta\pi_t$ will be equal to J_t/J_o . This enables $\sigma\Delta\pi$ to be eliminated from Equations 2 and 3, allowing the expression of L_p solely in terms of J_o , J_t and P (Eq. 4).

$$L_p = (J_t^2 - J_o^2)/J_t\Delta P \quad (4)$$

This is based on the assumption that root transport can be considered a composite process of distinct apoplastic and symplastic pathways for water movement (Steudle and Peterson, 1998). We have also assumed that, during measurements of EF, the osmotic component of Equation 1 would have been minimal, by ensuring that roots remained moist, and that transpiration rates were high (Fiscus, 1975). Under such conditions Q should be primarily responsive to ΔP and changes in root conductance produced by root chilling.

Low-pressure suction has been used to investigate root resistance (Mees and Weatherley, 1957), although the variable resistances reported in their study and by subsequent higher pressure techniques led to a number of papers probing the causes and effects of this feature of root behavior (Fiscus, 1975; Passioura, 1984; Steudle and Peterson, 1998). The issue of variable root conductivity remains unresolved, and according to the large body of data from experiments in which root pressurization was used to measure conductance, the low pressures used here should produce erroneously low conductances because of non-linearity in the response of root tissue to hydrostatic pressure gradients. This was not the case, however, and the root and shoot conductivities measured corresponded well with whole-plant conductivity determined by the EF technique over a range of sizes and of species.

Changes in the xylem resistance of plants were quantified by comparing observed water potential gradients across the plant with those expected from conductivity measurements from the same individuals. Manipulation of root conductance by chilling enabled whole-plant conductivity to be determined at a range of root to Ψ_l gradients and the effects of xylem cavitation to be assessed.

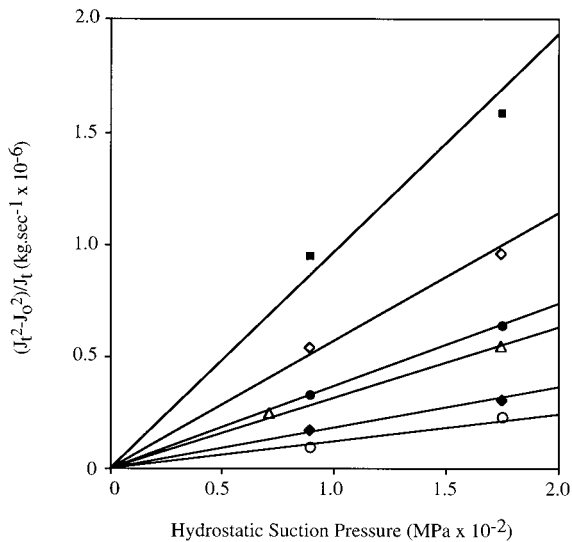


Figure 1. Hydrostatic suction applied to the root stump versus hydraulic flux minus osmotic flux (see Eq. 4) in six specimens of *E. regnans* with leaf areas ranging from 0.17 to 0.95 m². Regressions have been forced through zero. There is no evidence of non-linearity in the response of flux to applied pressure.

RESULTS

Root Conductivity

Root conductivity of individuals remained constant over the small range of tensions applied (Fig. 1). There was more than 1 order of magnitude range in the values of absolute root conductance and leaf area specific root conductance (Table I); however, there was only a relatively small amount of variation in K_r within species. K_r in the two conifer species were within the range of the two angiosperms, both on a leaf area and root dry-weight basis.

Root Chilling and Whole-Plant Conductivity

Root chilling caused an immediate decrease in Ψ_1 and transpiration, which stabilized usually within 30 min. The largest decreases were observed in *Toona australis* plants, which always wilted severely during root chilling (Fig. 2). Neither the angiosperm *Eucalyptus regnans* nor the conifers *Dacrycarpus dacry-*

dioides and *Nageia fleurii* were observed to wilt, although Ψ_1 did decline by 0.2 to 0.4 MPa in these species. In all species except *T. australis*, the effect of root chilling on Ψ_1 was close to the predicted value, assuming that root conductance was reduced by only the increased viscosity of water during chilling (Fig. 3). During root chilling in *T. australis*, however, measured Ψ_1 was substantially lower than the expected value (Fig. 3), indicating increased resistance somewhere in the hydraulic pathway. Rewarming of roots reversed this deviation from expected Ψ_1 in *T. australis* within 2 h (Fig. 4).

Stem vulnerability to cavitation was found to vary substantially between species. *T. australis* was extremely sensitive to pressure-induced cavitation, with a 50% loss of stem conductivity occurring at -1.45 MPa, which was within the measured values of Ψ_1 during root chilling. All other species showed little cavitation within the water potential range produced by root chilling (Table I).

DISCUSSION

Low-pressure suction proved to be an easy and effective means of quantifying root conductivity in four woody tree species including two conifers. There was a good correlation between observed and expected Ψ_1 in all species under non-cavitating xylem tensions, although whole-plant conductivities calculated from Ψ_1 were generally slightly higher than those calculated from root, stem, and leaf conductivities (Figs. 3 and 4). One possible reason for this is that root conductivity may decline in response to the release of water tension after detopping (Steudle and Peterson, 1998), and it was noted that conductivity did decrease significantly in the 1st h after shoots were detached. Rapid measurements were made during this 1st h to calculate maximum root conductivity, although there was still up to 35% difference between the observed and expected Ψ_1 . Another possibility is that Ψ_1 measured by the pressure bomb was not accurate in transpiring leaves (Melcher et al., 1998), although this suggestion has recently been strongly challenged (Wei et al., 1999).

Problems associated with non-linearity in the response of hydraulic flux to applied pressure were

Table I. Root and shoot conductance parameters for two angiosperm and two conifer species

Mean root conductance \pm SE ($n = 3$) is expressed in terms of leaf area (K_r) and whole root dry weight (K_{rdw}); stem conductivity (K_s) in terms of leaf area; and leaf hydraulic conductance (K_{leaf}). The mean \pm SE ($n = 3$) $\Psi_{cav50\%}$ can be considered the negative of stem water potential resulting in 50% cavitation.

Species	$K_r \times 10^{-5}$	$K_{rdw} \times 10^{-7}$	$K_s \times 10^{-5}$	$K_{leaf} \times 10^{-5}$	$\Psi_{cav50\%}$
	$\text{kg m}^{-2} \text{MPa}^{-1} \text{s}^{-1}$	$\text{kg MPa}^{-1} \text{s}^{-1} \text{g}^{-1}$	$\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$	$\text{kg MPa}^{-1} \text{m}^{-2} \text{s}^{-1}$	MPa
<i>E. regnans</i>	12.7 \pm 2.5	19.2 \pm 4.3	26.5 \pm 2.1	21.31 \pm 4.2	2.7 \pm 0.17
<i>T. australis</i>	2.51 \pm 0.28	4.40 \pm 0.9	17.8 \pm 1.7	16.28 \pm 0.7	1.4 \pm 0.20
<i>N. fleurii</i>	2.01 \pm 0.24	1.53 \pm 0.5	5.90 \pm 0.61	5.56 \pm 0.8	3.7 \pm 0.20
<i>D. dacrydioides</i>	1.86 \pm 0.26	3.90 \pm 0.7	7.24 \pm 0.76	7.46 \pm 0.7	2.3 \pm 0.20

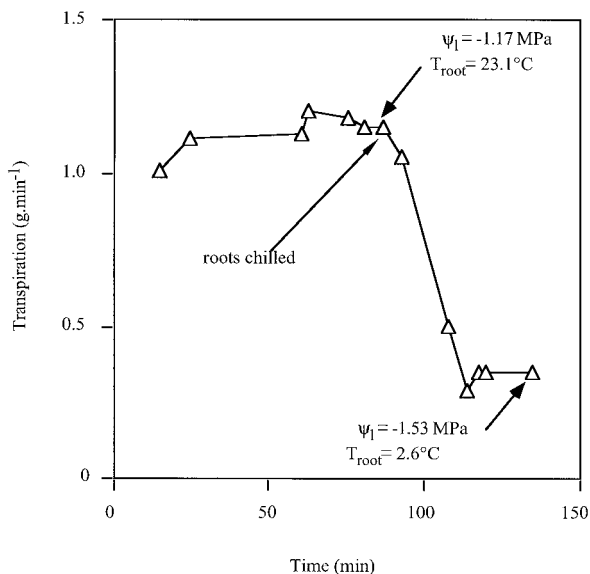


Figure 2. Changes in transpiration and Ψ_1 in response to root chilling in *T. australis*. Air temperature and humidity were maintained constant during the measurement period, indicating that changes in transpiration were largely due to decreases in stomatal conductance. Note that readings of root temperature, transpiration, and Ψ_1 were made after 20 min of steady-state EF.

overcome by assuming that the $\Delta\pi$ at 0 hydrostatic pressure was effectively diluted in proportion to the increase in J resulting from applied pressures (Eq. 4). Root conductivities calculated by this method remained constant over the small range of tensions used here (Fig. 1). These assumptions should have

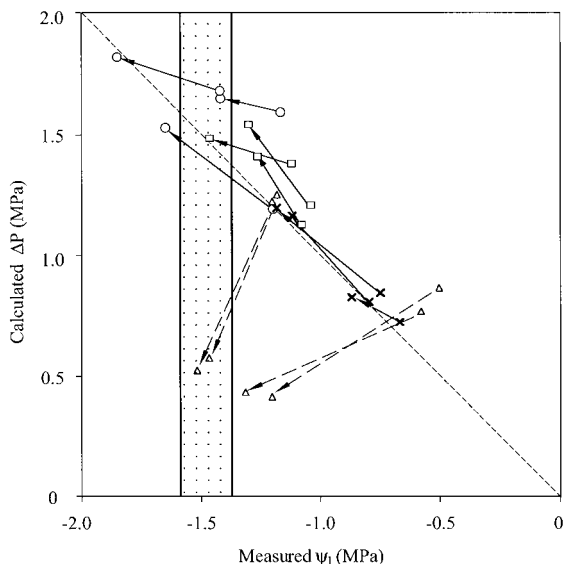


Figure 3. Calculated ΔP versus measured Ψ_1 in *E. regnans* (\times), *T. australis* (Δ), *D. dacrydioides* (\square), and *N. fleurii* (\circ). Arrows indicate the change in Ψ_1 before and during root chilling in the various individuals. The stippled region of the graph indicates the mean $\Psi_{cav50\%} \pm SE$ for *T. australis*. $\Psi_{cav50\%}$ in other species was less than -2 MPa. Note that only in *T. australis* does predicted ΔP deviate strongly from measured Ψ_1 after root chilling.

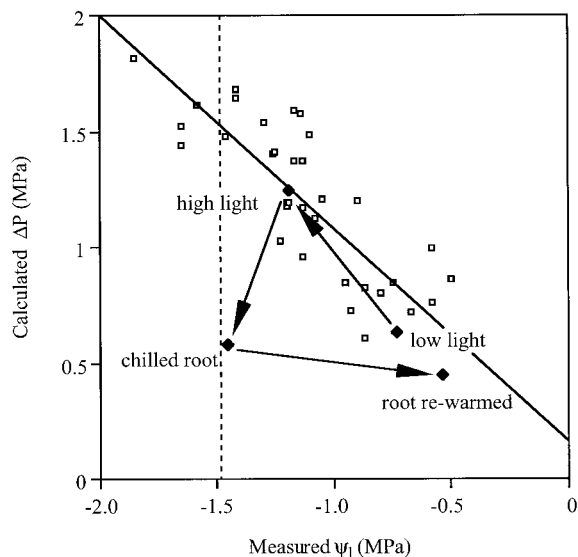


Figure 4. There was a highly significant ($P < 0.001$) correlation between measured Ψ_1 and calculated ΔP in pooled data from unchilled *T. australis* and all measurements from *E. regnans*, *D. dacrydioides*, and *N. fleurii* (\square). The slope of this regression is not significantly different from -1 . Also shown is the change in measured and calculated ΔP in a single specimen of *T. australis* (\blacklozenge) starting at low light ($50 \mu E m^{-2} s^{-1}$), then chilled roots ($5.8^\circ C$), and finally low light with roots rewarmed. Root chilling in *T. australis* caused Ψ_1 to approach $\Psi_{cav50\%}$ (marked with a dashed line).

been valid under the experimental conditions used, i.e. low soil π and high water potential during root conductivity and EF measurements and continual referencing of passive hydraulic flux when $\Delta P = 0$.

Values of whole-root conductivity determined here ranged from a maximum in *E. regnans* of 12.7×10^{-5} to a minimum of $1.86 \times 10^{-5} \text{ kg s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$ in the conifer *D. dacrydioides*. These values are consistent with data using the high-pressure flow meter technique for tropical tree seedlings (Tyree et al., 1998b) and fall within the large range of K_r produced by root pressure chamber measurements (Lo Gullo et al., 1998; Huxman et al., 1999). Considering the large difference between the maximum tension applied here (0.0175 MPa) and the positive pressures of generally between 0.1 and 0.5 MPa used in other whole-root methods, the agreement in these data adds confidence in the validity of both low- and high-pressure techniques.

In the two conifer species and *E. regnans*, chilling roots caused a decrease in K_r due to increased fluid viscosity. This in turn caused Ψ_1 to decrease and stomatal conductance to decrease in response (Figs. 2 and 3). The observed decline in Ψ_1 corresponded very closely to that expected if K_r was affected by changing viscosity alone. In these species, decreases in root conductance during chilling caused transpiration and Ψ_1 to decrease, but Ψ_1 did not approach a water potential resulting in 50% loss of stem conductance ($\Psi_{cav50\%}$, measured in megapascals). In *T. australis*, however, the increased water potential gradient pro-

duced by root chilling was much higher than that expected by viscosity changes alone. This substantial decrease in plant conductivity was probably due to large decreases in xylem conductivity due to cavitation. Support for this hypothesis comes in fact that stem xylem vulnerability to cavitation by water tension was extremely high in *T. australis* (Table I) and Ψ_1 was always near or below $\Psi_{\text{cav}50\%}$ during root chilling.

If the observed decrease in whole-plant conductance in this species was due to a combination of viscosity effects and cavitation in the stem xylem, then it would represent approximately a 95% loss of stem conductivity. This is possible given the very rapid decrease in stem conductivity typically observed once $\Psi_{\text{cav}50\%}$ is exceeded (Pammenter and Vander Willigen, 1998), although measurements of embolism by flushing (Sperry et al., 1988) in *T. australis* indicated only a 50% to 65% loss in stem conductivity after chilling (T.J. Brodribb, unpublished data). Another possibility is that cavitation in root and petiole xylem may have contributed to the loss in conductivity as it is likely that either of these could be more susceptible to cavitation than stem tissue. According to the vulnerability segmentation theory (Tsuda and Tyree, 1997) roots are the least vulnerable and petioles the most vulnerable to cavitation, although there is evidence to the contrary (Sperry and Saliendra, 1994; Hacke and Sauter, 1996). Other observations that covering leaves had no significant effect on Ψ_1 during root chilling (T.J. Brodribb, unpublished data) suggest that the major loss of conductivity occurred in the stem or root xylem.

These results provide evidence that xylem cavitation can exert a strong influence over Ψ_1 and whole-plant conductivity in vivo. Previously the only evidence of cavitation in living plants has been the detection of acoustic emissions (corresponding to cavitation events) from stems (Jackson et al., 1995). The rapid reduction in stomatal conductance by *T. australis* in response to root chilling was not rapid enough to prevent significant xylem cavitation, indicating that this species operates with a narrow safety margin before catastrophic xylem dysfunction (Tyree and Sperry, 1988). This is consistent with the ecological niche of *T. australis* as a fast growing rainforest pioneer (Herwitz, 1993), and in agreement with other studies that have detected cavitation in similar pioneer species when exposed to relatively small water potential deficits (Schultz and Matthews, 1997).

Root conductivity of the two conifer species here were within the range of the two angiosperms both on a leaf-area and dry-mass basis. This has been shown in other studies, although the data are limited (Sands et al., 1982; Rudinger et al., 1994; Becker et al., 1999). The absence of vessels in conifer roots probably does not produce a significant impediment to water flow in young plants at least, because the radial resistance in small root systems is substantially

higher than axial resistance, and vessels only affect higher axial hydraulic conductivity. The fact that no evidence of cavitation was observed in *E. regnans* or either of the two conifer species indicates that a more substantial safety margin exists between operating Ψ_1 and $\Psi_{\text{cav}50\%}$ in these taxa (Table I). In conifers this may be due to the fact that low root pressures make embolism repair inefficient and, hence, the xylem is more resistant to water stress-induced cavitation than associated angiosperm taxa (Sperry and Tyree, 1990; Tyree et al., 1998a). *E. regnans*, on the other hand, produces a high conductivity and root pressure, and relatively cavitation-resistant xylem, giving it the capacity for extremely high growth rates, but these characters probably contribute to its low shade tolerance (Van Der Meer et al., 1999).

In summary it was found that low-pressure suction was a simple and effective means of quantifying root hydraulic conductivity, yielding values of K_r that agreed with whole-plant measurements using the EF technique. Root chilling in *T. australis* caused Ψ_1 to approach or exceed $\Psi_{\text{cav}50\%}$ resulting in a substantial decrease in whole-plant conductivity, presumably by xylem cavitation. Quantification of the change in whole-plant conductivity during root chilling may provide a useful technique for measuring the relative safety margins within which plant species operate.

MATERIALS AND METHODS

Plant Material

Seeds from angiosperm wet-forest pioneers, *Eucalyptus regnans* and *Toona australis*, and the rainforest conifers, *Nageia fleurii* and *Dacrycarpus dacrydioides*, were germinated in sand and transferred to a pine-bark/sand potting medium in 5-L pots. Three plants of each species were grown under natural light conditions in a heated greenhouse until they reached a size of between 1 and 1.5 m tall.

Whole-Plant Conductance and Manipulation of Root Conductance

EF was measured in individually potted plants, in the greenhouse under conditions of full-sun or under metal halide lamps producing a photosynthetic photon flux of 500 to 600 $\mu\text{E m}^{-2} \text{s}^{-1}$ and approximately 25°C and 35% to 45% relative humidity. Prior to measurement, plants were soaked with water, and pots were covered with plastic bags to eliminate water loss. Transpiration was measured gravimetrically, with average rates calculated every 10 to 15 min depending on rates of evaporation. When the EF had stabilized for at least 30 min, three leaves (or leaflets) were detached for Ψ_1 measurements. Pots were then removed from the balance and iced water flowed through them until root temperature had decreased to between 2°C and 5°C. Soil temperature was recorded by four thermocouples inserted among the roots. Temperature measurements on the stems of plants during chilling indicated that the chilling effect was largely confined to the roots, with stem

temperatures increasing to 20°C at a height of approximately 10 cm above the soil. After the plants had cooled, they were placed in an insulated container on the balance, and EF was monitored for 2 h, or until a new steady state had been reached. After the chilled-root steady state was reached, an additional three leaves were removed for Ψ_1 measurement and soil temperature recorded. In one individual of each species, four leaves were wrapped in laboratory film (Parafilm, American National Can, Greenwich, CT) and foil during the early morning, and Ψ_1 was measured on these wrapped leaves during maximum transpiration at mid-day. Ψ_1 of these leaves were compared with Ψ_1 in uncovered leaves to calculate a mean leaf hydraulic conductivity for each species. All Ψ_1 data were collected using a Scholander-type pressure bomb with a dissecting microscope attached for precise determination of the end point.

Plants were allowed to recover from root chilling for 5 to 10 d before they were harvested for measurement of shoot and root conductivity.

Shoot Conductivity and Vulnerability

To measure conductivity across the bulk of the shoot, stem segments were cut as long as possible, running from the base of the shoot to the tip of a terminal branch. Side shoots were all removed and plugged with Teflon tape and petroleum jelly. Conductivity was measured by applying a hydrostatic pressure of 6 kPa to the base of the segment and measuring the efflux of water on an electronic balance. Conductivity was expressed as the hydraulic flux (kilograms per second) divided by the pressure gradient across the stem (megapascals per meter) and also as the leaf-area specific conductivity by dividing by the leaf area supplied by the stem segment.

After conductivity was measured, stems were placed into a 15-cm-long double-ended pressure bomb (Sperry and Saliendra, 1994) and flushed with filtered water at 0.175 MPa until conductivity remained at a maximum stem hydraulic conductance prior to air injection (K_m , kilograms per second per megapascal per meter). Following this, chamber pressure was gradually increased to 0.50 MPa for 20 min and released, and conductivity was remeasured. This process was continued at 0.50-MPa increments until conductivity declined to 5% of K_m . Applied pressure was then plotted against the percentage loss of conductivity relative to K_m at each pressure, and a regression was fitted assuming a loss of conductivity by a cumulative normal curve shape (Brodribb and Hill, 1999). From these curves the $\Psi_{\text{cav}50\%}$ was interpolated.

Root Conductivity

Plants were detopped under water during mid-morning. Stumps were quickly shaved with a razor and attached to a length of tubing filled with degassed water. Tubing led to a pipette whose tip was submerged in a reservoir of water placed on a computer-interfaced balance. Air temperature in the laboratory was controlled to 22°C, and root temperature was monitored by four thermocouples placed around

the root. Roots remained in soil, but were continually bathed by a slow flow of water, ensuring that the soil remained fully saturated and the osmotic potential of the soil was a minimum. Initially a hydrostatic pressure of -0.0175 MPa was applied by placing the surface of the water reservoir 1.78 m below the center of gravity of the pot. Balance readings of the mass of water exuded were made every 2 min, and as soon as the hydraulic flux stabilized (usually 10 min) the pot and balance were leveled and the hydraulic flux was remeasured. A second tension of 0.009 MPa was then applied and the flux was remeasured. Several measurements were made at each of the two tensions while passive flow from the roots was regularly referenced. Immediately after a pressure change, hydraulic flux was unstable, decaying to a steady state within 5 to 10 min; hence, measurements of hydraulic flux were made at these steady states. Usually it was the case that both root pressure and conductivity decreased slowly after detopping, and hence only the initial two to three measurements were averaged to produce a value for whole-root conductivity. Tensions of more than -0.0175 MPa resulted in air being drawn through the root, and hence this was the maximum suction applied to the root.

It was assumed that the flux of solutes into the root vascular stele responsible for passive flow when $\Delta P = 0$ remained constant between passive flow measurements and small applied tensions, and hence, Equation 2 was used to calculate whole-root conductivity. Conductivities were all normalized to the water viscosity at 20°C. No attempt was made to quantify root area; thus, root conductivities were either expressed as kilograms per second per megapascal and matched to EF data expressed on a leaf-area basis (K_r) or root dry-weight basis for comparisons between individuals (Tyree et al., 1998b).

EF versus Hydraulic Conductivity Data

Comparison of EF and hydrostatic conductivity measurements were made by using the whole-plant conductivity (combined K_r , leaf hydraulic conductivity, and stem hydraulic conductivity) for each individual to calculate the expected soil-leaf ΔP (equal to Ψ_1 under the saturated soil conditions used here) at each observed EF. This expected ΔP was compared with the average Ψ_1 determined from the pressure bomb. It was assumed that, during rapid transpiration while the pot was soaked with water, the osmotic gradient across the root was low and that soil water potential was approximately zero.

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