Tree Physiology 27, 1389–1400
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Dynamic variation in sapwood specific conductivity in six woody species

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Received December 11, 2006; accepted January 19, 2007; published online July 3, 2007

Summary Our goals were to quantify how non-embolism-inducing pressure gradients influence trunk sapwood specific conductivity (k_s) and to compare the impacts of constant and varying pressure gradients on k_s with KCl and H_2O as the perfusion solutions. We studied six woody species (three conifers and three angiosperms) which varied in pit membrane structure, pit size and frequency of axial water transport across pits (long versus short conduits). Both stepwise ("steady") and nonlinear continuous ("non-steady") decreases in the pressure gradient led to decreased k_s in all species but white oak (*Quercus garryana* Dougl. ex Hook), a ring-porous and long-vesseled angiosperm. In one diffuse-porous angiosperm (red alder, *Alnus rubra* Bong.) and two conifers (western red cedar, *Thuja plicata* Donn. ex D. Don, and Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco), k_s was 10–30% higher under steady pressure gradients than under non-steady pressure gradients, and a decrease in the pressure gradient from 0.15 to 0.01 MPa m^{-1} caused a 20–42% decrease in k_s. In another diffuse-porous angiosperm (maple, *Acer macrophyllum* Pursh) and in a third coniferous species (western hemlock, *Tsuga heterophylla* (Raf.) Sarg), there was no difference between k_s measured under steady and non-steady pressure gradients. With the exception of western red cedar, a conifer with simple pit membranes, the differences in k_s between low and high pressure gradients tended to be lower in the conifers than in the diffuse-porous angiosperms. In Douglas-fir, western red cedar and the diffuse-porous angiosperms, k_s was higher when measured with KCl than with H_2O. In white oak, there were no differences in k_s whether measured under steady or non-steady pressure gradients, or when xylem was perfused with KCl or H_2O. The species differences in the behavior of k_s suggest that elasticity of the pit membrane was the main factor causing k_s to be disproportionate to the pressure gradient and to the different pressure regimes. The results imply that, if nonlinearities in pressure–flux relationships are ignored when modeling tree water relations in vivo, large errors will result in the predictions of tree water status and its impact on stomatal control of transpiration and photosynthesis.

Keywords: Darcy's law, hydraulic architecture, non-steady, steady, tracheids, vessels, xylem.

Introduction

The specific conductivity (k_s) of wood to liquid, a transport property that is necessary for accurate understanding and modeling of long distance water flow in plants, should be measured under conditions that recreate the transient behavior of water movement in vivo. Steady-state techniques have traditionally been employed for determining k_s, mainly because of their simplicity in theory and calculations. Steady state exists when the volumetric flow rate (Q) through a porous medium is constant. Although several studies have been undertaken on the mechanisms affecting steady-state flow of liquids in wood (Bolton and Petty 1978, Bolton 1988), we found only one study on non-steady-state flow of liquids through wood (Lin and Lancaster 1973). Flow through porous media can be described by a combination of the Darcy equation (Darcy 1856) and the continuity equation (conservation of mass when a fluid is in motion; Fetter 2001), with k_s regarded as a function of wood structure. This empirically determined equation, which has since been derived from simplified Navier-Stokes equations (Carmen 1956, Hager and Gisonni 2002), relates the laminar flow rate of a liquid to the pressure gradient (change in hydraulic head over a distance) and k_s under steady-state conditions:

$$Q(l,t) = \frac{k_s A \partial P(l,t)}{\eta \partial l} \quad (1)$$

where A is the area across which the flow occurs, P is the liquid phase pressure, η is the liquid dynamic viscosity and l is the length of the flow path.

Following Darcy's original work, much experimental and analytical work has been devoted to the application of Darcy's law to the description of the flow of liquids through wood

(Muskat 1982). However, there are many violations to Darcy's law when applied to water flow in living trees and key aspects of the relationships between pressure gradients and flow rates are not well understood (Bramhall 1971, Kramer 1983). The main violation occurs when k_s is determined by steady-state methods and the values obtained are applied to a living system in a continuous non-steady-state regime. For example, the inappropriate use of coefficients derived from steady-state measurements can result in both underestimates (Tyree et al. 1994) and overestimates (Lin and Lancaster 1973) of conductivity of living systems. Although some tree physiologists have recognized explicitly that flow and pressure gradients in trees are not normally in steady state (Booker 1977, Giordano et al. 1978, Sperry and Tyree 1990), this condition has been more widely acknowledged in the wood processing literature (Resch 1967, Siau and Shaw 1971, Banks 1981). Steady-state flow rarely occurs in trees because any or all of the following can change with time: A (Tognetti et al. 1998, Eckmüllner and Sterba 2000); η (Cochard et al. 2000), ΔP (Hinckley et al. 1994, Meinzer et al. 1995, Brodribb and Hill 2000); and the effect of dynamic discharge and recharge of water stored in capillary space, conduit lumens (Goldstein et al. 1998, Meinzer et al. 2003) and xylem ray parenchyma (Holbrook 1995). Some plant physiologists have inadvertently measured k_s under non-steady-state flow because their methods could not maintain steady flows. They have specified criteria for designating a sufficiently stable flow at which to measure k_s, and termed it "quasi-steady-state" (Bréda et al. 1993, Yang and Tyree 1994, Tyree et al. 1995, Cochard et al. 1997).

The second violation of Darcy's law when applied to living trees is that k_s is often determined in vitro at pressure gradients (0.03 to 0.10 MPa m^{-1}) exceeding those that exist in trees (< 0.03 MPa m^{-1}, Bauerle et al. 1999, Woodruff et al. 2004, Domec et al. 2005). If the resulting values of k_s are pressure gradient dependent, they may not explain the behavior of water transport in trees. One study investigating the pressure dependence of k_s in wood found decreasing flow rates at constant pressure and disproportionate increases with increasing pressure (Bailey and Preston 1970). The effects were explained by pit aspiration, or plugging of pit membranes, or both. Sperry and Tyree (1990) also reported an increase in conductivity at low pressure gradients in *Acer saccharum* Marsh. and *Juniperus virginiana* L., but provided no explanation for such results (see Figures 12a and 12b in Sperry and Tyree 1990). At high pressure gradients not likely to be found in intact trees, an opposite response, a decrease in flow rate with increasing applied pressure, was observed by Sucoff et al. (1965), Sperry and Tyree (1990) and Lu and Avramidis (1999). They concluded that the decrease in flow resulted from turbulence or pit closures, or both, rather than air blockages. We hypothesize that the main cause for the flow rate to be disproportionate to pressure is that pit membranes become distorted as they are distended elastically. In an un-aspirated pit, the membrane would occupy a medial position in the pit chamber before the application of force (Figure 1a). If the pressure is higher within one conduit than in the adjacent one, the fibers holding the membrane would behave like uniformly loaded beams fixed at both ends. As the membrane begins to distend (Figure 1b), the pores become larger so the flow path will become less restricted. As the membrane distends even further (Figure 1c), the downstream channel between the membrane and the pit borders will restrict flow (Figure 1c). Therefore, at low pressure differentials we could expect an increase in k_s because of increased bordered pit conductance, but if the pressure continued to increase, k_s would decrease.

The third violation of Darcy's law occurs when k_s is measured with deionized water because xylem sap ionic composition and pH can affect xylem conductivity (Zimmermann 1978, Van Ieperen 2000, Zwieniecki et al. 2001). Increasing KCl concentration in the perfusion solution during measurements of hydraulic conductivity caused a more than 2.5-fold increase in k_s in some angiosperm species, but had a minimal effect in conifer species. Because the response was localized in pit membranes, Zwieniecki et al. (2001) suggested that perfusing solutions caused pectins in the membranes to swell or shrink, thereby altering the size of the membrane microchannels.

Because of the complexity of the observed pressure–flow relationships, studies using methods that reproduce the relevant in vivo conditions on the excised wood segments studied in the laboratory are needed to gain a better understanding of the physics of fluid in the xylem. The goals of our study were to assess the impact of dynamic variation in pressure gradients on flow through xylem varying in structure, and to determine the effects of xylem sap composition on these results. We expected that: (1) k_s would vary with the pressure gradient; (2) k_s

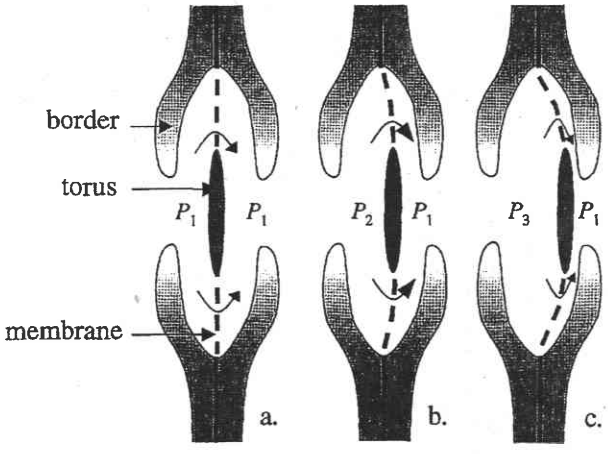

Figure 1. Proposed model to explain the variation in flow rate and specific conductivity as the pressure gradient between two adjacent conduits increases. The diagram shows a section through a bordered pit pair, with the midline being the compound middle lamella of two adjacent conduits and the pit membrane. The relative volume of water flow through the small pores of the bordered pit membrane as pressure increases from P_1 to P_2 to P_3 is represented by the size of the arrowheads. Although only a coniferous bordered pit with a central thickening (torus) in its membrane is shown, the model would be the same for coniferous or angiosperm bordered pits with a simple membrane.

would depend on whether the pressure gradient was steady or non-steady; and (3) the magnitude of differences in k_s resulting from changes in pressure regime would depend on the ionic strength of the perfusion solution. We compared results in three coniferous and three angiosperm species from the Pacific Northwest with disparate conduit and pit characteristics to further generalize conclusions about the role of pit border and membrane types.

Material and methods

Wood material and sample preparation

We studied three angiosperms and three gymnosperms with contrasting wood anatomy (Table 1) that were available locally in the McDonald-Dunn Forest near the Oregon State University campus. Among the angiosperms, Oregon white oak (*Quercus garryana* Dougl. ex Hook) is ring-porous, and as such, has long vessels and a large range of vessel diameters (Table 1). Bigleaf maple (*Acer macrophyllum* Pursh) and red alder (*Alnus rubra* Bong.) are both diffuse-porous. It is likely that pit pore sizes decrease from bigleaf maple (the most water-requiring species) to red alder, then white oak. Pit morphology varies markedly among the gymnosperms studied. Bordered pits in Douglas-fir (*Pseudostuga menziesii* (Mirb.) Franco) have a larger diameter, thicker torus and more margo strands than those in western hemlock (*Tsuga heterophylla* (Raf.) Sarg) (Bauch et al. 1972). Western red cedar (*Thuja plicata* Donn. ex D. Don) is one of the few North American conifers with simple pit membranes lacking torus and margo; it consists of numerous, closely packed strands (Krahmer and Côté 1963).

Healthy mature trees, free of broken tops and stem deformities, were selected based on cambial age estimated from increment cores. Between July and September 2004, we felled four individuals of each species. We sampled two locations within the outer sapwood of each tree to limit variability. Immediately after felling, we cut a 25-cm thick disk from the base of each tree. The disks were transported in wet polyethylene bags to the laboratory, and stored at 3 °C until blocks were prepared within three hours of felling. Both ends of each disk were covered with wet paper towels to limit evaporation from the xylem. From each disk, four 180–200-mm-long blocks were cut from the outer part of the sapwood at regular intervals around the circumference. Following the procedures outlined by Spicer and Gartner (1998) and Domec and Gartner (2001), the blocks were split along the grain first with a maul and wedge, and then smoothed with a chisel to create axially oriented beams, 1.4 × 1.4 cm in the tangential and radial directions, and 15 cm in the tree's axial direction. The current year (2004) was excluded in order to have samples with complete annual growth rings (5 to 12 depending on the species). The entire cross-sectional area of each sample block was assumed to be functional sapwood and was calculated from the mean of the cross-sectional areas of the two ends.

Before being tested, the samples were soaked in water and put under a vacuum for at least 48 hours to remove the existing emboli in order to determine k_s values at full saturation. To test for complete refilling, the relative water content of each sample (the proportion of non-cell-wall space that is occupied by water) was calculated after the final measurement and ranged from a minimum value of 96 ± 4% in red alder to a maximum value of 99 ± 2% in western hemlock. Samples were recut at both ends and the cut surfaces smoothed with razor blades to a final length of 10.1–10.3 cm. Measurements of k_s were made with a membrane-lined pressure sleeve that held a latex sleeve against the exposed axial edges of the sample to ensure that fluid did not leak from the sides of samples (Spicer and Gart-

Table 1. Morphological characteristics of sampled trees and saturated specific conductivities (k_s) at low (0.013 MPa m^{-1}) and high (0.160 MPa m^{-1}) steady pressure gradients with deionized water as the perfusion fluid and corrected to 20 °C (mean ± SE, $n = 4$). Values of k_s with different letters within a column or row are significantly different ($P < 0.05$).

	White oak (*Quercus garryana*)	Bigleaf maple (*Acer macrophyllum*)	Red alder (*Alnus rubra*)	Western hemlock (*Tsuga heterophylla*)	Douglas-fir (*Pseudotsuga menziesii*)	Western red cedar (*Thuja plicata*)
Tree age (years)	108 ± 9	58 ± 5	43 ± 1	51 ± 3	46 ± 3	49 ± 4
Diameter at breast height (cm)	22.3 ± 2.2	29.6 ± 3.4	29.5 ± 0.9	30.2 ± 1.1	39.8 ± 0.8	24.1 ± 1.9
Tree height (m)	19.4 ± 1.1	26.5 ± 0.7	28.1 ± 0.6	34.0 ± 2.2	33.5 ± 0.9	16.3 ± 1.3
Conduit diameter (μm)	210–222[1]	65–80[2]	55–65[3]	30–45[4]	35–50[5]	28–35[4]
Conduit length (mm)	500–2500[6]	40–250[2]	30–150[6,7]	2.2–2.9[8]	2.6–3.1[5]	2.1–2.7[5]
k_s high (kg m^{-1} s^{-1} MPa^{-1})	11.1 ± 1.1 a	4.3 ± 0.2 b	3.5 ± 0.2 c	3.1 ± 0.3 cd	4.1 ± 0.2 b	1.8 ± 0.1 f
k_s low (kg m^{-1} s^{-1} MPa^{-1})	10.8 ± 1.1 a	3.5 ± 0.3 c	2.9 ± 0.1 de	2.6 ± 0.3 e	3.8 ± 0.3 c	1.4 ± 0.1 g

[1] Lei et al. (1996).
[2] Watson et al. (1988).
[3] Gartner et al. (1997).
[4] Panshin and deZeeuw (1980).
[5] Domec et al. (2006*b*).
[6] Authors' unpublished observations.
[7] Deal and Harrington (2006).
[8] Siripatanadilok and Leney (1985).

ner 1998). Although the latex membrane was pressurized to 0.05 MPa, this pressure does not affect the flow rate through the samples (Spicer and Gartner 1998, authors' unpublished observations). Hereafter, we refer to this apparatus as "the holder." For all experiments, one end of the holder was attached by tubing to a reservoir filled with deionized and filtered (0.22 μm) water or 25 mmol KCl made with deionized and filtered water. The flow of solution through the segments was in the same direction as in the intact plant. Flow rate was determined by an electronic balance (± 0.1 mg) connected to a computer (Sperry et al. 1988).

The temperature of the solution was recorded before and after each k_s measurement and varied by no more than 0.5 °C during any one experiment. Fluid viscosity was corrected to 20 °C for all reported k_s values. Before and after each measurement, we determined the flow rate in the absence of an applied pressure head. This zero-pressure "background" flow has been shown to be zero (Cavender-Bares and Holbrook 2001) or small and negative because water can enter the samples in the absence of a pressure head (Kolb and Sperry 1999). In our study, the background flow was zero because the height of the water reservoir was adjusted to the height of the sample, and probably also because the samples were enclosed in the holder, which prevented them from losing water during the experiment.

Experiment 1: non-uniformity of specific conductivity under steady pressure gradients

The magnitude of the pressure gradient was controlled by adjusting the height of the fluid reservoir. The sample was positioned at the same height as the downstream height. Pressure on the upstream end of the stem segment was estimated as atmospheric pressure plus the hydraulic head produced by a water column over the vertical distance between the supply reservoir and the sample, and pressure on the downstream end was taken as atmospheric pressure. On the first subsample per tree, measurements were made starting from a maximum pressure head of 1.63 m (16 kPa), reducing stepwise to a value of 0.13 m, and then increasing stepwise to the initial pressure head. There were a total of six pressure steps between the maximum and the minimum pressure values. At each step, flow occurred for 5 min before measurements were taken, then efflux was collected for a minimum of 5 min more. On the second subsample, measurements were made starting from the lowest pressure head, increasing stepwise and then reducing stepwise to the initial height. Two to three cycles were undertaken per sample.

Experiment 2: non-uniformity of specific conductivity under non-steady and quasi-steady pressure gradients

The same samples as those used in Experiment 1 were connected to a pressurized chamber for determination of k_s with a nonlinear rate of pressure change (adapted from Lin and Lancaster 1973, Figure 2). The apparatus consisted of a pressure tank divided into two chambers separated by an impermeable rubber membrane. The first chamber, which was connected to the sample, was filled with deionized filtered water, included a pressure transducer (± 0.1 kPa, PX 135-015, Omega Engineering, Stamford, CT). The second chamber was filled with air and was attached to a cylinder of compressed air. The pressure in the water-filled chamber was adjusted by increasing or decreasing the volume of air in the second chamber.

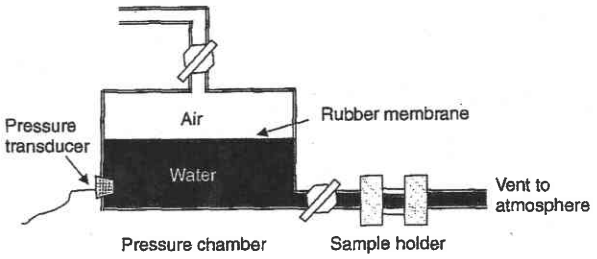

Figure 2. Diagram of the pressurized chamber apparatus used to measure conductivity under non-steady pressure gradients.

The liquid was pressurized before the sample was attached. As soon as liquid began to flow through the sample, the pressure in the chamber decreased, creating a non-steady pressure gradient. The relationship between time and the change in water pressure (measured by the pressure transducer) was used to estimate k_s under non-steady pressure gradient conditions (see Equation 4 below). Flow through the sample created a feedback between the pressure and flow because the volume of water that passed through the sample was equivalent to the increase in the volume of air in the air chamber. Because samples were at full saturation, we assumed that the xylem water content remained constant across all applied pressures (no capacitive discharge or recharge) and that changes in k_s were the only cause of the changes in flow rate at a given transient pressure. Using the derivative form of Darcy's law and calling P_o the atmospheric pressure and dv the volume of water flowing through the sample during the small interval of time dt:

$$dv = \frac{k_s A(P - P_o)}{\eta l} dt \tag{2}$$

Assuming that air in the upper chamber behaves as an ideal gas, then $PV = nRT$, where n is the quantity of gas (moles) and R is the gas constant. The water temperature was assumed equal to that of the air in the adjacent chamber. This assumption is based on the premise that expansion occurred slowly and that the heat capacity of the chamber was sufficient to buffer temperature changes due to changes in gas pressure. Given that $V = C/P$, we have that $dv = -C/P^2 dP$ and Equation 2 can be rewritten as:

$$\frac{-dP}{P^2(P - P_o)} = \frac{k_s A}{C\eta l} dt \tag{3}$$

Calling P_i the initial pressure at $t = 0$, we can integrate from $t = 0$ to t and from P_i to P (during these experiments, we used a P_i of 0.02 MPa):

$$\frac{1}{P_o^2}\ln\frac{P}{P-P_o}-\frac{1}{P_oP}=\frac{k_sA}{C\eta l}t+\left(\frac{1}{P_o^2}\ln\frac{P_i}{P_i-P_o}-\frac{1}{P_oP_i}\right) \quad (4)$$

We calculated k_s from the slope (S) of the plot of

$$\frac{1}{P_o^2}\ln\frac{P}{P-P_o}-\frac{1}{P_oP}$$

against time, given that A, C, η and l are known, k_s was determined as:

$$k_s=\frac{\eta lCS}{A} \quad (5)$$

The plot of

$$\frac{1}{P_o^2}\ln\frac{P}{P-P_o}-\frac{1}{P_oP}$$

versus time was often nonlinear with respect to pressure change because of non-constant k_s with applied pressure, but followed instead a quadratic polynomial relationship. The slope in Equation 5 at any applied pressure was then determined using the derivative of this quadratic polynomial curve. Specifically, S was calculated as t, the time elapsed from P to P_o, times the derivative at t of this quadratic polynomial curve. Therefore, by developing a simple relationship, it was possible to estimate conductivity coefficients under non-steady pressure gradients without having to employ the more complex and time-consuming numerical methods analysis.

In addition, for methodological and comparative purposes, we collected water efflux on a balance to determine k_s with Equation 1 when using the pressurized chamber. These values, referred to as k_s under "quasi-steady" pressure gradients, were computed based on the mean pressure difference and the amount of water collected during time intervals ranging from 10 s at maximum pressure to 1 min at low pressure. The values of k_s measured under quasi-steady pressure gradients were then compared with k_s determined under non-steady pressure gradients.

Statistical analysis

Because all measurements were made on the same samples, paired t-tests were performed to assess differences between the k_s values resulting from different pressure gradient manipulations, and to determine if there was an effect on k_s of the perfusion fluid used. We used the analyses to compare k_s measured under non-steady, quasi-steady and steady pressure gradients. Differences between species (Table 1) were determined by a one-way analysis of variance (ANOVA).

Results

During the steady pressure gradient measurements, k_s always declined within the first hour of measurements, whether we used deionized water or KCl as the perfusion fluid. The example for deionized water in Figure 3 shows that maximum values of k_s during the first pressure cycle (between 0 and 150 min) were always greater than maximum values during subsequent pressure cycles. This pattern was observed for every species studied but it was more pronounced in conifers.

No significant hysteresis ($P > 0.45$) was detected in the response of k_s to increasing or decreasing steady pressure gradients (Figure 4), indicating that the increase in k_s did not result from conduit refilling associated with increasing pressure. Pressure-dependent variation in k_s measured under quasi-steady pressure gradients followed the trends of k_s measured under non-steady pressure gradients regardless of whether we used KCl or H_2O (Figure 5).

In the ring-porous species, white oak, the difference in k_s between low and high pressure gradients was not significant ($P > 0.67$, Table 1). In this species, there was also no significant difference ($P > 0.19$) in k_s measured either under steady or non-steady pressure gradients, or with KCl or H_2O as the perfusion fluid (Figure 6).

In both of the diffuse-porous species, bigleaf maple and red alder, there was an asymptotic increase in k_s with increasing pressure gradients under both flow regimes (Figure 6). At high pressure gradients, k_s was significantly higher than at low pressure gradients for both kinds of perfusion fluid ($P < 0.03$) and for both kinds of flow regime ($P < 0.04$). In bigleaf maple and red alder, k_s measured at the highest pressure gradient (0.160 MPa m^{-1}) was significantly higher than any k_s measured at a pressure gradient lower than 0.063 MPa m^{-1}. Similarly, k_s measured at the lowest pressure gradient (0.013 MPa m^{-1}) was significantly lower than any k_s measured at a pressure gradient higher than 0.046 MPa m^{-1}. In addition, for these two species, k_s was significantly higher when perfused with KCl than when perfused with H_2O ($P < 0.05$). In red alder, k_s was significantly higher ($P < 0.03$) when measured under steady pressure gradients than under non-steady pressure gradients for both kinds of perfusion fluid. For this species, the increase in k_s between low and high pressure gradients under

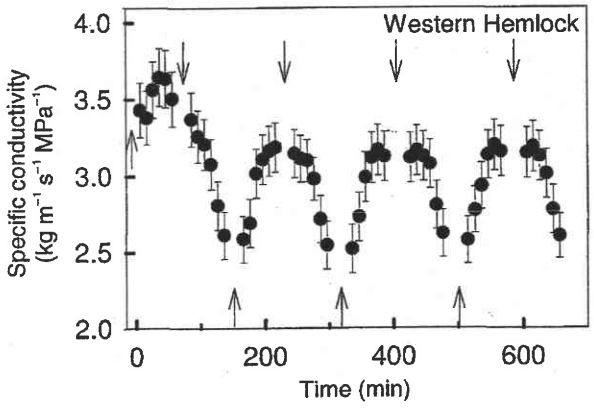

Figure 3. An example showing specific conductivities (k_s) of western hemlock stem xylem measured under steady pressure gradients as a function of time with deionized water as the perfusion fluid (mean ± SE, $n = 4$). The arrows show when the pressure gradients were increasing (up) or decreasing (down).

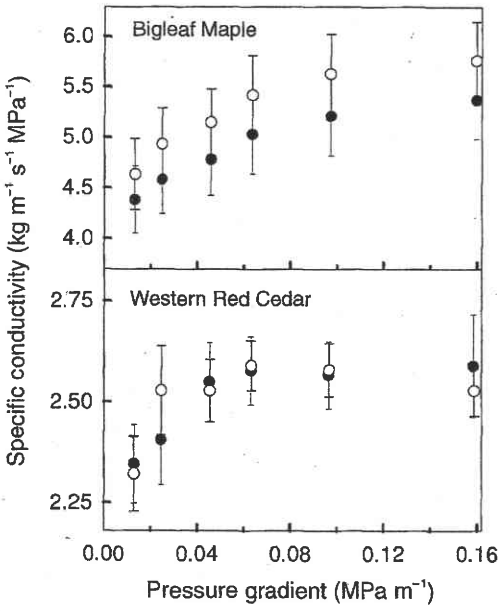

Figure 4. Specific conductivities of stem xylem under steady pressure gradients as a function of an increasing (●) or a decreasing (○) pressure gradient with 25 mmol KCl as the perfusion fluid (mean ± SE, $n = 4$).

non-steady pressure gradient was significantly lower ($P < 0.01$) when using H_2O than when using KCl and ranged from 42% with H_2O to 74% when using KCl. Under a steady

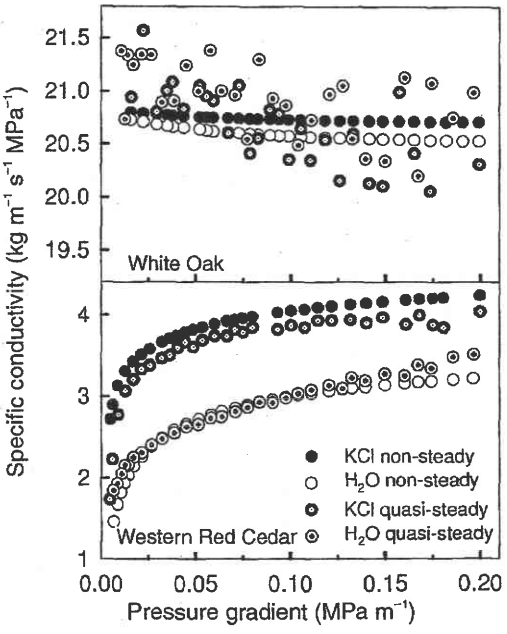

Figure 5. Specific conductivities of stem xylem in relation to non-steady and quasi-steady pressure gradients measured with the pressurized chamber using either 25 mmol KCl or deionized water as the perfusion fluid.

pressure gradient, the increase in k_s between low and high pressure gradients in red alder was of the same order of magnitude regardless of whether we used KCl or H_2O and ranged from 12 to 17% (Table 1). In bigleaf maple, there was no significant difference ($P > 0.10$) in k_s measured under either steady or non-steady pressure gradients (Figure 6). In bigleaf maple, the difference in k_s at low and high pressure gradients was of the same order of magnitude regardless of whether we used KCl or H_2O, and ranged from 22 to 25% under a steady pressure gradient (Table 1) and from 39 to 43% under a non-steady pressure gradient.

In the three conifers, there was an asymptotic relationship between k_s and the pressure gradient (Figure 7), with values of k_s being significantly greater at high pressure gradients than at low pressure gradients for both pressure regimes ($P < 0.04$) and both perfusion fluids ($P < 0.02$). For example, in western hemlock and Douglas-fir, k_s measured at the highest pressure gradient was significantly higher than any k_s measured at a pressure gradient lower than 0.046 MPa m^{-1}, and k_s measured at the lowest pressure gradient was significantly lower than any k_s measured at a pressure gradient higher than 0.063 MPa m^{-1}. In western red cedar, k_s measured at the highest pressure gradient was significantly higher than any k_s measured at a pressure gradient lower than 0.063 MPa m^{-1} and k_s measured at the lowest pressure gradient was significantly lower than any k_s measured at a pressure gradient higher than 0.046 MPa m^{-1}. In western hemlock, there was no difference ($P > 0.35$) between k_s measured under steady or non-steady pressure gradients, and the difference between the minimum and maximum k_s ranged between 14 and 20% and was smaller than in the other two conifer species. In Douglas-fir and western red cedar, k_s measured with either KCl or H_2O under steady pressure gradients was significantly higher ($P < 0.04$) than k_s measured under non-steady pressure gradients (Figure 7) with the largest differences occurring at the lowest pressure gradients (less than 0.02 MPa m^{-1}). In Douglas-fir, there was an 8% increase in k_s from the lowest to highest pressure gradient under steady pressure gradients (Table 1) and a 50% increase under non-steady pressure gradients and the relative increase in k_s between low and high pressure gradients was of the same order of magnitude regardless of whether we used KCl or H_2O. Moreover in Douglas-fir, under non-steady state pressure gradients, k_s measured with KCl was not significantly different from k_s measured with H_2O ($P > 0.14$). In western red cedar, k_s increased by 28% under steady pressure gradients and by 40% under non-steady pressure gradients. In addition, for this species, the increase in k_s between low and high pressure gradients measured either under steady or non-steady pressure gradients was significantly lower ($P < 0.02$) when using KCl than when using H_2O and ranged from 10 to 39% when using KCl and from 28 to 65% when using H_2O.

Discussion

Differences in k_s measured at a given pressure gradient

Under both steady and non-steady pressure regimes, the spe-

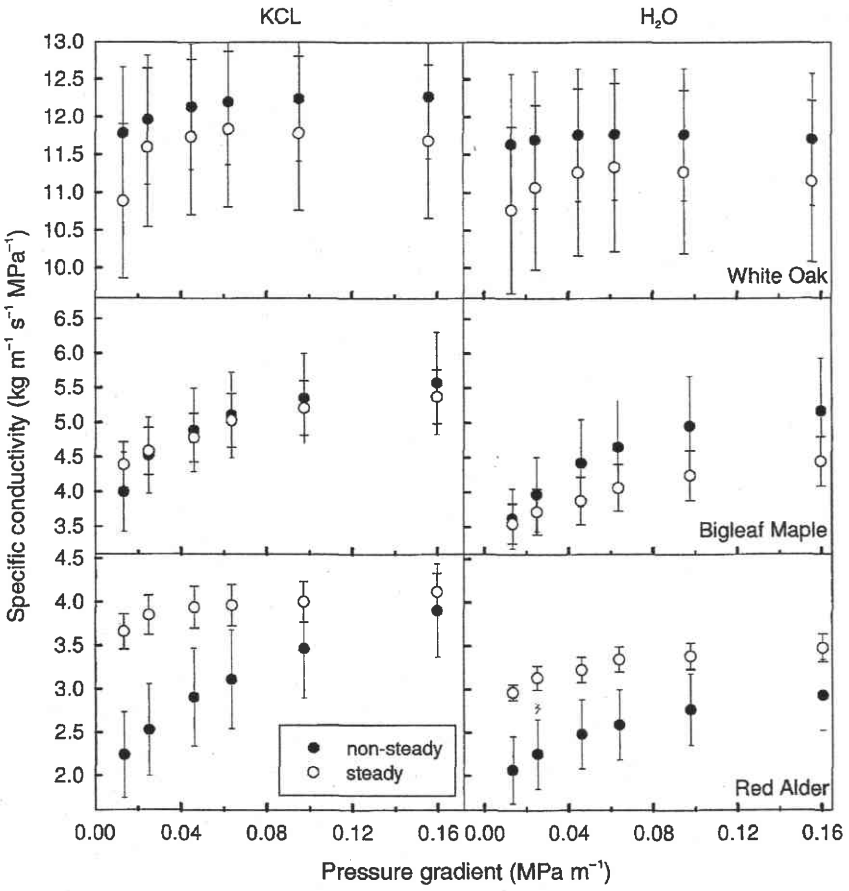

Figure 6. Specific conductivities of angiosperm stem xylem in relation to steady and non-steady pressure gradients using either deionized water (H_2O) or 25 mmol KCl as the perfusion fluid (mean ± SE, $n = 4$).

cific conductivity (k_s) of fully hydrated wood increased with increasing pressure gradient; i.e., liquid flow rates increased more than expected from Darcy's law as applied pressure increased. This observation is consistent with prior evidence that, in some cases, xylem water flux is not a linear function of the applied pressure (Peel 1965, Sucoff et al. 1965, Bailey and Preston 1970, Giordano et al. 1978). The mechanisms responsible for this nonlinearity are not yet clearly understood, but various mechanisms have been proposed, including air blockages and pit closure, as well as non-laminar (turbulent) flow. Irreversible pit aspiration and closure occurring at high pressure gradients may explain why conductivities decline within the first hour of measurements and become constant for a given pressure gradient thereafter (Figure 3). When the flow is turbulent, the flow contains unsteady vortices that interact with each other and k_s declines (Rott 1990). Because our results showed that with increasing pressure gradients, k_s was greater rather than lower, it is unlikely that turbulent flow occurred at high pressure gradients.

Instead, we propose that the main cause for the nonlinear relationship between flow rate and pressure gradient is that pit membranes become distorted and their conductivity changes as they distend elastically (Figure 1). If the strain of the stretched membrane is in the elastic range, then a total recovery will occur when the force is removed (Sperry and Tyree 1990), which explains the non-hysteretic reversibility of changes in k_s as pressure gradients are either lowered or raised (Figure 4). The increase in k_s could be caused by expansion of the membrane pores when the membrane distends, thus reducing the bordered pit resistance to flow. The incremental deflection of pit membranes decreases with increasing increments of applied pressure (Sperry and Hacke 2004), which could explain the asymptotic increase in k_s with pressure gradient. At pressure gradients higher than 0.1 MPa m^{-1}, we hypothesize that, although increasing pit membrane pore size results in increased k_s, deflection of the entire membrane reduces the channeled water flow between the membrane and the edge (borders) of the pit (Figure 1c).

An inverse relationship between the pressure gradient and k_s has been reported in some gymnosperms (Sperry and Tyree 1990) and one angiosperm (Sherwin et al. 1998) and was ascribed in the gymnosperms to the increased pressure forcing the torus against the pit border. However, the pressure gradients used in earlier experiments were an order of magnitude higher than the ones we used, and were imposed on branches, which necessarily have lower flow rates and lower k_s than most stem sections because of their much smaller tracheids (Domec and Gartner 2002, Dunham et al. 2007). A slight decrease in k_s at high pressure gradients was also occasionally seen in our study when comparing pressure gradients above 0.1 MPa m^{-1}.

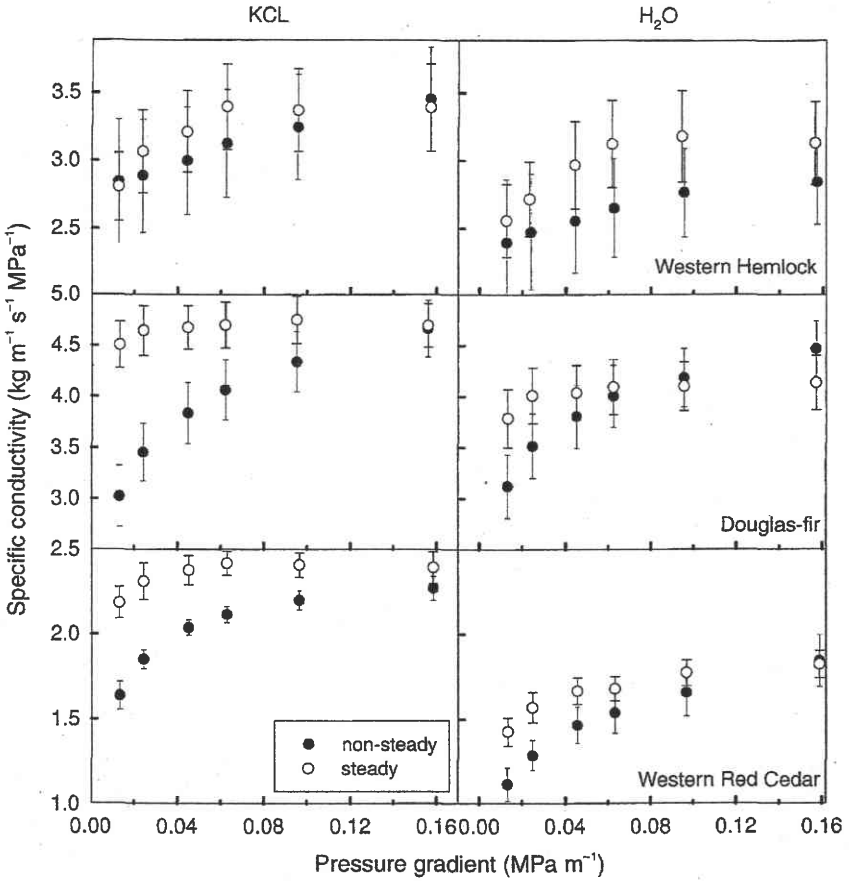

Figure 7. Specific conductivities of conifer stem xylem in relation to steady and non-steady pressure gradients during perfusion with either deionized water (H_2O) or 25 mmol KCl as the perfusion fluid (mean ± SE, $n = 4$).

Differences in k_s between steady-state and non-steady-state pressure regimes and consequences for water transport in living trees

As far as we are aware, this is the first report of interspecific comparisons of k_s measured under steady and non-steady pressure regimes. We hypothesize that most of the deviations from Darcy's law between steady and non-steady pressure regimes can be accounted for by changes in pit membrane function under different pressures and flow rates. The material that makes up pit membranes is similar to primary cell wall material and thus should exhibit rapid and appreciable deflections under low loadings. Lin et al. (1973) attributed the difference in behavior under steady and non-steady pressure regimes to pit membrane flexibility and to the delayed response (hysteresis) between the time the pressure is applied and the time the membrane starts moving. Thus, in this view, under a non-steady pressure gradient, the membranes can occupy a continuum of positions (Fengel 1972), resulting in hysteresis, which would lead to lower k_s values compared with steady pressure gradients because the pores would not stretch instantaneously with the increase in pressure gradient. Because bigleaf maple and western hemlock showed no differences between steady and non-steady pressure regimes, we predict that the pit membranes of these species are flexible and respond quickly to pressure changes.

The effect of steady versus non-steady pressure gradients on k_s differed in conifers and angiosperms, and is also probably related to differences in their bordered pit structure. Because the mean diameter of the pit membrane is much smaller than that of the conduit lumens, k_s is largely dependent on the size and structure of the bordered pits (Pittermann et al. 2005). In both angiosperms and conifers the bordered pits can represent at least 50% of the total xylem resistance (Sperry et al. 2005, Domec et al. 2006*a*). In angiosperms, calculations based on morphological features of bordered pits have shown that a significant fraction of the limiting flow resistance of bordered pit membranes is located in the pit membrane pores rather than the aperture (Schulte and Gibson 1988, Sperry and Hacke 2004, Hacke et al. 2006). In contrast, in conifers, the pit aperture has been shown to represent more than two thirds of the total pit resistance (Lancashire and Ennos 2002, Hacke et al. 2004, Domec et al. 2006*a*). These results may explain why, with the exception of western red cedar, the differences in k_s between low and high pressure gradients tended to be lower in the conifers than in the diffuse-porous angiosperms studied. Western red cedar pit membranes consist of numerous microfibrils without a distinct torus (Krahmer and Côté 1963, Liese and Bauch 1967), and so the main resistivity may occur in membrane pores, as we hypothesize to be the case in the diffuse-porous angiosperm species. In other words, the majority of pit resistivity in conifers is associated with the pit border, and therefore, the membrane distension at different pressure

gradients will have only a minimal impact on pit resistance. In addition, because they lack a torus and margo (Jansen et al. 2004), simple pit membranes found in most angiosperms and a few conifers like western red cedar are easier to deflect than bordered pit membranes (Sperry and Hacke 2004, Hacke et al. 2004). Thus, in contrast to the case in the typical conifer, the diffuse-porous species and western red cedar resistivity would be much more dependent on distension of the pit membrane, which we have hypothesized to be nonlinear with changes in the pressure gradient (Figure 1).

White oak, a ring-porous species with long vessels, provides a test for our hypothesis that pit characteristics determine the response of k_s to variations in the pressure gradient and steady- versus non-steady-state regimes. In contrast to the diffuse-porous species, the samples of oak were shorter than the minimum vessel length (Greenidge 1952, Zimmermann 1983, Sano 2005), so very few pit membranes had to be crossed by the liquid. Therefore, the necessity of crossing more pit membranes per meter of sap ascent in the diffuse porous species would be expected to increase the dependence of xylem k_s on the pressure gradient and on the type of pressure regime (Figure 6).

A recent study of Douglas-fir showed that pores within the pit membrane represent 30% of the pit resistance and around 25% of the total resistance (Domec et al. 2006*a*). To obtain a mean increase in k_s of around 8% from low to high steady pressure gradients (Table 1), margo pore resistivity would have to decrease by 32% upon stretching. The membrane resistivity scales with the diameter of the pores to the third power, and therefore an increase in pore diameter due to membrane stretching of only 10% would decrease margo resistivity by 32%. A difference of 0.14 MPa m^{-1} in pressure gradient (intermediate between the extremes of the gradients measured in this study) would give a difference across a single tracheid of 0.4 kPa. In Douglas-fir, this pressure drop would correspond to a membrane displacement of around 15% of its maximum displacement (from normal to aspirated position), which may be sufficient to increase pore diameter and increase overall k_s by 10% (Domec et al. 2006*a*). These values are in agreement with those reported by Bolton and Petty (1978), who found that a membrane displacement of 10% occurs at a pressure difference across a single tracheid of 0.1 kPa. Previous estimates of pressure differences to initiate deflection in conifer membranes range from 7.5 to 15 kPa (Sperry and Tyree 1990), but theses values represented the threshold pressures at which k_s started to decrease. Such pressure differences would represent a membrane displacement of 40–50% and we think that, in such a position, the increase in pore size would be counteracted by the reduction in flow between the membrane and the border of the pit (Figure 1c).

In western hemlock, k_s increased 15–20% between low and high pressure gradients, which would require a larger increase in pore diameter with increasing pressure gradient than in Douglas-fir. Although this species has a distinct torus with margo strands, the diameter of the torus is usually smaller with a denser margo and smaller pores compared with that of Douglas-fir. In addition, incrustations in the membranes are often present (Krahmer and Côté 1963, Bauch et al. 1972, authors' unpublished observations), which are likely to increase the influence of margo pores on the overall bordered pit resistivity, and the differences in k_s between low and high pressure gradients.

The maximum pressure gradient tested in the experiments was more than would occur in a transpiring hydrated plant, so that the actual k_s under these conditions may be more than the maximum occurring in situ. The main changes in k_s occurred at low pressure gradients, which are of the same order of magnitude as those occurring in living trees (Bauerle et al. 1999, Domec and Gartner 2002). An actively transpiring tree with trunk or foliage water potentials in the range of –1 to –2 MPa experiences pressure gradients of 0.01 to 0.02 MPa m^{-1} in conifers (Woodruff et al. 2004, Domec et al. 2006*b*) and 0.04 MPa m^{-1} in maple and alder (Fallas-Cedeño 2005). Thus it is likely that an intact transpiring tree will have a lower k_s than that measured in the laboratory, which is often measured at gradients between 0.05 and 0.1 MPa m^{-1}. Because the steady-state method is the simplest option to determine k_s, we suggest that scientists standardize the measurement of k_s by generating steady-state conductivity at pressure gradients encountered in the field by the plant organ studied. This approach would limit the potential error when evaluating and interpreting water transport in intact trees based on k_s measurements in excised xylem. Numerous studies have generated steady-state conductivity measurements to calculate leaf specific conductivity or tree hydraulic conductance in an attempt to model water transport and to estimate whole-tree water use in vivo (e.g., Tyree 1988, Sperry et al. 2002, Tyree 2003, Sobrado 2003, Domec et al. 2005, Maseda and Fernández 2006). The differences in k_s between steady and non-steady pressure gradients as well as between low and high pressure gradients observed in the present study imply that some earlier studies may have significantly overestimated xylem capacity to supply water to transpiring leaves and consequently whole-tree water use.

Discrepancies in k_s values measured under steady-state and non-steady-state conditions may also be problematic for the interpretation of xylem vulnerability from embolism curves. As tension in the water column increases, vessels and tracheids become embolized (air-filled), and k_s declines (Zimmermann 1983). The vulnerability curve is a plot of percent loss of k_s as a function of tension in the water column. Thus, the steady-state values of k_s traditionally measured during vulnerability curve determination may not be representative of the consequences of embolism for water transport under the dynamic conditions that prevail in intact plants.

Perfusion liquid and difference in steady and non-steady k_s

A limited number of studies on the influence of fluid ionic composition on k_s have shown that the presence of cations in the permeating solution increases k_s by reducing the resistance to flow at the pit membrane via shrinkage of pectins imbedded in the membrane (Van Ieperen et al. 2000, Zwieniecki et al. 2001). It is possible that the influence of pressure gradients on

membrane pore size may differ according to whether the pectins are swollen or shrunken. Because the effect of fluid ionic composition is localized to pit membrane pores, its influence on k_s has been shown to be more important in angiosperms than in conifers (Zwieniecki et al. 2001), which explains why large differences were found in both of the diffuse porous species and also why white oak showed no differences (few membranes were crossed). In many conifer species, pit membranes in the sapwood contain pectins but no phenolic substances (Bauch and Berndt 1973), which may explain why western hemlock did not respond to a change in fluid composition whereas Douglas-fir did. Finally, the response of western red cedar to KCl or deionized H_2O was comparable with the response of both diffuse-porous species. We hypothesize that this similarity was due to the lack of a torus in the bordered pits of western red cedar, and the existence of a membrane anatomically comparable with that found in angiosperms, with the probable presence of pectic substances.

Acknowledgments

This work was supported by USDA-CSREES NRI 03-35103-13713 the USDA Forest Service Ecosystem Processes Program (PNW 02-JV-1126952-252) and a special USDA grant to OSU for wood utilization research. Sincere thanks to J.M. Warren for his assistance with tree felling at McDonald-Dunn Forest, Corvallis, OR.

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