

## Dynamic variation in sapwood specific conductivity in six woody species

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**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<sub>2</sub>O 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-vessel 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<sup>-1</sup> 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<sub>2</sub>O. 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<sub>2</sub>O. 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,  $\eta$  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, Eckmüller and Sterba 2000);  $\eta$  (Cochard et al. 2000),  $\Delta P$  (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)  $k_s$

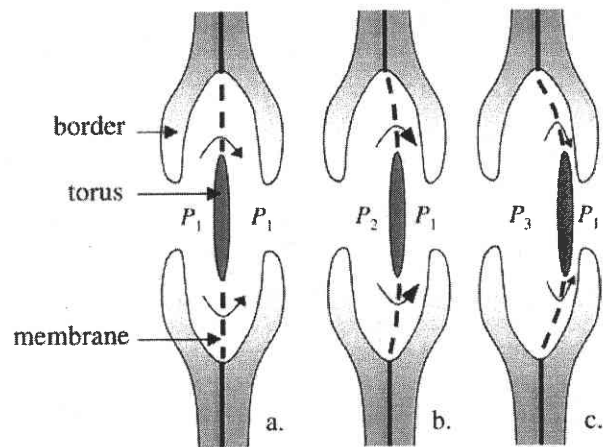


Figure 1. Proposed model to explain the variation in flow rate and specific conductivity as the pressure gradient between two adjacent conduits increases. The diagram shows a section through a bordered pit pair, with the midline being the compound middle lamella of two adjacent conduits and the pit membrane. 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 (*Pseudotsuga 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 incre-

ment 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<sup>-1</sup>) and high (0.160 MPa m<sup>-1</sup>) 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 ( <i>Quercus garryana</i> )	Bigleaf maple ( <i>Acer macrophyllum</i> )	Red alder ( <i>Alnus rubra</i> )	Western hemlock ( <i>Tsuga heterophylla</i> )	Douglas-fir ( <i>Pseudotsuga menziesii</i> )	Western red cedar ( <i>Thuja plicata</i> )
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 <sup>1</sup>	65–80 <sup>2</sup>	55–65 <sup>3</sup>	30–45 <sup>4</sup>	35–50 <sup>5</sup>	28–35 <sup>4</sup>
Conduit length (mm)	500–2500 <sup>6</sup>	40–250 <sup>2</sup>	30–150 <sup>6,7</sup>	2.2–2.9 <sup>8</sup>	2.6–3.1 <sup>5</sup>	2.1–2.7 <sup>5</sup>
$k_s$ high (kg m <sup>-1</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	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 <sup>-1</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	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

<sup>1</sup> Lei et al. (1996).

<sup>2</sup> Watson et al. (1988).

<sup>3</sup> Gartner et al. (1997).

<sup>4</sup> Panshin and deZeeuw (1980).

<sup>5</sup> Domec et al. (2006b).

<sup>6</sup> Authors' unpublished observations.

<sup>7</sup> Deal and Harrington (2006).

<sup>8</sup> 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  $\mu\text{m}$ ) 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 ( $\pm 0.1$  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  $^{\circ}\text{C}$  during any one experiment. Fluid viscosity was corrected to 20  $^{\circ}\text{C}$  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

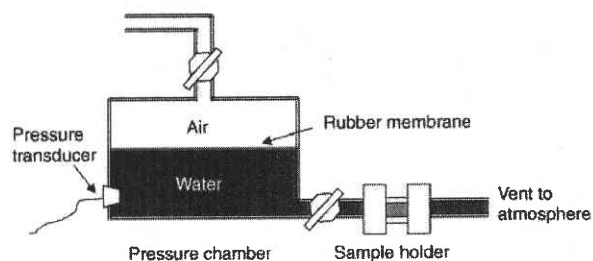


Figure 2. Diagram of the pressurized chamber apparatus used to measure conductivity under non-steady pressure gradients.

the sample, was filled with deionized filtered water, included a pressure transducer ( $\pm 0.1$  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.

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  $P_0$  the atmospheric pressure and  $dv$  the volume of water flowing through the sample during the small interval of time  $dt$ :

$$dv = \frac{k_s A (P - P_0)}{\eta l} dt \quad (2)$$

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:

$$\frac{-dP}{P^2 (P - P_0)} = \frac{k_s A}{C \eta l} dt \quad (3)$$

Calling  $P_1$  the initial pressure at  $t = 0$ , we can integrate from  $t = 0$  to  $t$  and from  $P_1$  to  $P$  (during these experiments, we used a  $P_1$  of 0.02 MPa):

$$\frac{1}{P_0^2} \ln \frac{P}{P-P_0} - \frac{1}{P_0 P} = \frac{k_s A}{C \eta l} t + \left( \frac{1}{P_0^2} \ln \frac{P_1}{P_1-P_0} - \frac{1}{P_0 P_1} \right) \quad (4)$$

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

$$\frac{1}{P_0^2} \ln \frac{P}{P-P_0} - \frac{1}{P_0 P}$$

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

$$k_s = \frac{\eta l C S}{A} \quad (5)$$

The plot of

$$\frac{1}{P_0^2} \ln \frac{P}{P-P_0} - \frac{1}{P_0 P}$$

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  $P_0$ , 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 val-

ues 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<sub>2</sub>O (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<sub>2</sub>O 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<sup>-1</sup>) was significantly higher than any  $k_s$  measured at a pressure gradient lower than 0.063 MPa m<sup>-1</sup>. Similarly,  $k_s$  measured at the lowest pressure gradient (0.013 MPa m<sup>-1</sup>) was significantly lower than any  $k_s$  measured at a pressure gradient higher than 0.046 MPa m<sup>-1</sup>. In addition, for these two species,  $k_s$  was significantly higher when perfused with KCl than when perfused with H<sub>2</sub>O ( $P < 0.05$ ). 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

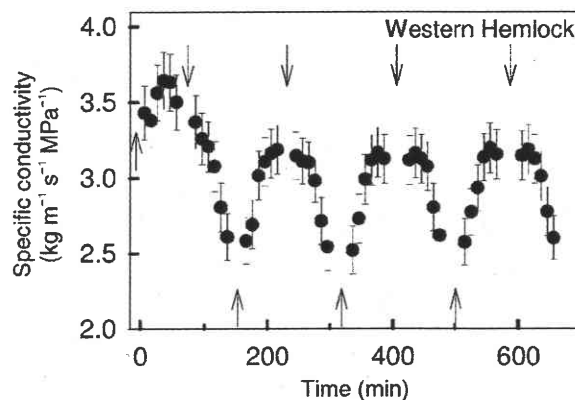


Figure 3. An example showing specific conductivities ( $k_s$ ) of western hemlock stem xylem measured under steady pressure gradients as a function of time with deionized water as the perfusion fluid (mean  $\pm$  SE,  $n = 4$ ). The arrows show when the pressure gradients were increasing (up) or decreasing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