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Xylem anisotropy and water transport-a model for the double sawcut experiment

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Summary Early experiments with overlapping cuts to the stems of trees demonstrated that lateral flow within the stem must be possible to allow such trees to maintain water flow to their leaves. We present a mathematical approach to considering lateral flow in stems by treating the xylem as an anisotropic medium for flow and develop an expression of its conductivity in the form of a tensor. In both 3D models of tracheid-bearing stems with cuts (incorporating this tensor analysis) and experimental stems with steadily deepening cuts, it is shown that flow can continue despite the presence of even strongly overlapping cuts through 90% of the stem. Such remaining conducting ability was, however, strongly dependent on values for radial and tangential conductivity (conductivity to lateral flow across the stem either radially with respect to the central axis or tangentially to the stem surface). Furthermore, the lateral flow around obstructing cuts was more dependent on tangential flow around the stem upstream and downstream of the cuts than on radial flow across the stem. The relative importance of tangential flow could be accounted for by a greater tangential conductivity, perhaps related to the predominance of pits on radial walls of tracheids, and the presence of non-conducting pith and early growth rings in the stems. These results demonstrate that a consideration of anisotropy in transport properties of the xylem will be important for future studies of flow in stems around naturally occurring geometric features such as branching points.

Keywords: anisotropic, conductivity, tensor, tracheid.

Introduction

Early studies of water flow through stems of large woody plants involved the creation of overlapping sawcuts to the stems of these trees in an attempt to understand the pathways for flow. For such studies utilizing either injected stains (Greenidge 1955) or radioactive tracers (Postlethwait and Rogers 1958), the cuts would presumably sever all direct vertical connections between roots and leaves, but nonetheless the leaves did not wilt. This result may have been thought initially to be evidence against the prevailing cohesion-tension theory of water ascent. However, careful experiments on the effects of distance between the cuts showed that cuts closer than some minimum separation associated with the length of individual vessels (occurring in the angiosperm species studied) did lead to wilting of the foliage because air bubbles were introduced, blocking flow in all vessels between the cuts (MacKay and Weatherly 1973). Thus, it became clear that flow around the cuts was made possible by lateral transfer between water-filled conduits of the xylem, although the conductivity to flow may be lower laterally than axially along the stem.

Such differences in lateral and axial conductivity also make sense for plants with xylem conduits like tracheids based on their anatomical characteristics. These cells are long and narrow (of the order of a few millimeters in length and tens of micrometers in diameter). Tracheids are also imperforate, and flow from cell to cell depends on pits in the cell walls. Roughly speaking, passage through one set of pits allows flow through the length of one cell. But for lateral flow perpendicular to the axis of the cell, flow through the pits of one cell only achieves a distance of one cell diameter. In addition among conifers with tracheids, pits are far more common on radial walls of the cells than on tangential walls (Siau 1971, Panshin and de Zeeuw 1980; radial walls are those oriented along a radial line out from the stem center). This consideration would suggest that lateral conductivity might be greater in the tangential direction than in the radial direction. Thus, based on the anatomy of conducting cells, one would obviously expect the xylem to be an anisotropic conducting medium, where conductance to flow depends on direction.

One expression of the anisotropic nature of plant xylem arises with the term sectoriality. If the lateral conducting ability across a cylindrical stem is sufficiently limited, the stem xylem is effectively isolated into sections tangentially around the stem. Numerous studies have suggested that sectoriality is variable among plants. Larson et al. (1993, 1994) have shown that long-lived individuals (>1000 years) of northern white

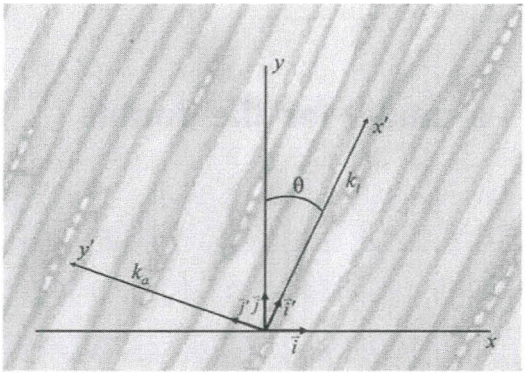

Figure 1. Coordinate axes for transformation. For the 2D case, the cell conducting property is oriented at some angle θ with regard to a standard coordinate system (x, y). The background image shows water-conducting tracheids of *Pinus strobus* L. xylem as viewed in the axial plane of the cells (tangential-longitudinal section of a cylindrical stem). Conductivity in the direction of the long axis of the cell is k_l and in the perpendicular direction across the cells is k_a.

cedar *(Thuja occidentalis* L.) found on limestone cliffs along the Niagara Escarpment in southern Ontario, Canada are highly sectored-individual roots are strongly connected with individual branches, and this characteristic may be important for their survival. Other studies have suggested that the xylem is well connected around the stem, and this degree of interconnectedness may be an important characteristic of plants for their adaptation to various environments (Zanne et al. 2006, Taneda and Tateno 2007). Therefore the previously cited experiments with overlapping cuts in the stem (after which at least some flow still continues), along with the more recent studies of sectoriality just described, suggest that the capability for lateral flow as well as flow along the stem is an important property of stems deserving further study.

The purpose of the present work was to develop an approach for incorporating the anisotropic nature of the xylem into a transport equation for flow and also to test this model experimentally. We revisit the double sawcut experiment by measuring the hydraulic conductance of stems while a series of stepwise cuts are made into the stem and from a mathematical perspective by creating models of cylindrical stems with cuts of various depths. Although this is obviously an artificial system, the authors hope to show that it can be useful for developing an approach incorporating anisotropic conductivity that will be applicable in more complex but naturally occurring systems such as branch junctions.

Theoretical development

Anisotropy and the hydraulic conductivity tensor

Mathematical descriptions and models have been useful tools for understanding the transport process in plants (Pickard 1981, Nobel 1991). For ID approaches including branched ID electrical circuit analog models, flow resistances or conductances are scalar quantities, although they may vary spatially. On the other hand, for many plant tissues, the geometric shapes of the cells and differences in cell wall properties among the various wall faces mean that the conducting ability for water flowing through the tissue depends on direction. These tissues are therefore said to be anisotropic with regard to conductivity, and this property is not a simple scalar quantity but must be described through tensor analysis. If the conducting medium is anisotropic, flow will depend on the orientation of the tissue together with the direction of applied driving forces for flow (a tensor is a mathematical construct used here to describe properties that depend on direction; see Ozisik 1968). The expression of conductivity as a tensor has often been a component in models of flow within the soil (e.g., Raats et al. 2004) or in drying lumber (e.g., Perre and Turner 2002, Truscott and Turner 2005), but to our knowledge, tensors have not been incorporated into models of flow within living plants. Therefore, the purpose of the present work is to develop mathematical applications of the anisotropy concept for water transport in the xylem of plants and to test such approaches by comparison with experimental stems bearing double cuts.

Reflecting the complexity of tissue geometry, the orientation of the cells often varies spatially, and thus it is important to consider separately a coordinate system with respect to cell orientation and a global coordinate system used in any analysis of tissues at a larger scale. The transformation between such coordinate systems leads to the generation of a conductivity tensor. Starting with a simple 2D case (see Figure 1) and neglecting changes in tissue water storage, the conducting medium for flow is anisotropic, and so flow in the x (or y) direction may be driven by forces in the x or y direction:

$$-q_x = k_{xx}\frac{\partial P}{\partial x} + k_{xy}\frac{\partial P}{\partial y}$$
$$-q_y = k_{yx}\frac{\partial P}{\partial x} + k_{yy}\frac{\partial P}{\partial y} \quad (1)$$

where q_i is the flow (volume flux; $m^3\ m^{-2}\ s^{-1}$ m s^{-1}) in the direction i, P is the pressure (MPa) or other driving force for flow in the x or y direction, and k_{ij} represents the conductivity ($m^2\ MPa^{-1}\ s^{-1}$) for flow in the i direction as driven by a force in *the j* direction. The conductivity tensor (K) for flow would be written as:

$$\underline{K} = \begin{bmatrix} k_{xx} & k_{xy} \\ k_{yx} & k_{yy} \end{bmatrix} \quad (2)$$

As noted above, the tissues are not necessarily oriented the same as applied driving forces for movement, and so these two different coordinate systems need to be considered.

In the $Ox'y'$ system (a local coordinate system oriented with respect to the cells), the conductivity tensor is:

$$\underline{K}' = \begin{bmatrix} k_l & 0 \\ 0 & k_a \end{bmatrix} \quad (3)$$

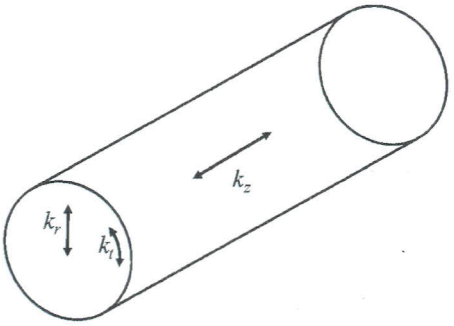

Figure 2. Cylindrical representation of a plant stem with conductivities in the axial (k_z), radial (k_r) and tangential (k_t) directions.

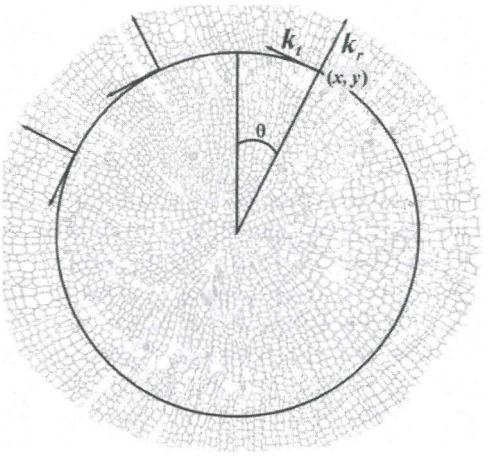

Figure 3. Circular cross-section through a representative conifer cylindrical stem, showing cell orientation as radial, with associated radial conductivity (k_r), or tangential, with associated tangential conductivity (k_t). Any given point on the section has coordinates (x, y), and the local conducting axis system ($Ox'y'$ from Figure 1) is oriented at the angle θ.

where the subscripts l and a refer to directions (in the $Ox'y'$ system) with the long axis of the cells and across the cells, respectively. We want a corresponding conductivity tensor in the Oxy system. The unit vectors $\vec{i}'$, $\vec{j}'$ oriented with respect to the cells (Figure 1) are given by

$$\begin{aligned}\vec{i}' &= (\sin\theta)\,\vec{i} + (\cos\theta)\,\vec{j} \\ \vec{j}' &= -(\cos\theta)\,\vec{i} + (\sin\theta)\,\vec{j}\end{aligned} \tag{4}$$

where $\vec{i}$, $\vec{j}$ are the reference unit vectors in the Oxy system. Note that Eq. (4) can be written as

$$\begin{bmatrix}\vec{i}' \\ \vec{j}'\end{bmatrix} = \begin{bmatrix}\sin\theta & \cos\theta \\ -\cos\theta & \sin\theta\end{bmatrix}\begin{bmatrix}\vec{i} \\ \vec{j}\end{bmatrix} = A\begin{bmatrix}\vec{i} \\ \vec{j}\end{bmatrix} \tag{5}$$

The conductivity tensor $\underline{K}$ in Oxy is given from

$$\underline{K} = A^{-1}\underline{K}'A \text{ where } A = \begin{bmatrix}\sin\theta & \cos\theta \\ -\cos\theta & \sin\theta\end{bmatrix} \tag{6}$$

We calculate:

$$\begin{aligned}\underline{K} = A^{-1}\underline{K}'A &= \begin{bmatrix}\sin\theta & -\cos\theta \\ \cos\theta & \sin\theta\end{bmatrix}\begin{bmatrix}k_l & 0 \\ 0 & k_a\end{bmatrix}\begin{bmatrix}\sin\theta & \cos\theta \\ -\cos\theta & \sin\theta\end{bmatrix} \\ &= \begin{bmatrix}\sin\theta & -\cos\theta \\ \cos\theta & \sin\theta\end{bmatrix}\begin{bmatrix}k_l\sin\theta & k_l\cos\theta \\ -k_a\cos\theta & k_a\sin\theta\end{bmatrix} \\ &= \begin{bmatrix}k_l\sin^2\theta + k_a\cos^2\theta & k_l\sin\theta\cos\theta - k_a\sin\theta\cos\theta \\ k_l\sin\theta\cos\theta - k_a\sin\theta\cos\theta & k_l\cos^2\theta + k_a\sin^2\theta\end{bmatrix}\end{aligned} \tag{7}$$

A tensor approach has also been used in a different context for models of soils (Russo et al. 1998) and of drying lumber (Perre and Turner 2002).

A cylindrical plant stem with radial and tangential cell orientations

For this application (Figure 2), the specific conductivities can be described along axial, radial and tangential directions. Biologically speaking, the cells are long relative to their width, and this long axis is oriented with the long axis of the stem cylinder. The cells of many conifers have roughly rectangular cross-sections with a pair of wall faces oriented along the radius and a pair of faces oriented tangentially with respect to the outer stem surface. These faces have different numbers of wall pits (Siau 1971, Panshin and de Zeeuw 1980) through which water flows from cell to cell, and hence the conductivities in the radial and tangential direction are not necessarily the same. The cells being much longer than wide means that a greater distance along the length of the stem can be covered without water having to cross through the wall, and so the conductivity in the axial direction is much greater than in either the radial or tangential directions. Although the cylindrical geometry might suggest a cylindrical coordinate system, the use of this approach here for a cylindrical stem with cuts from opposite sides (lacking cylindrical symmetry) and future uses for more complicated geometries such as the junctions associated with branching in stems removes the advantages of using a cylindrical coordinate system. Therefore, it will be useful to consider a Cartesian coordinate system globally while recognizing that anatomically it makes sense to express conductivity in radial and tangential directions.

The next task is to resolve the differences between the Cartesian coordinate system and the notions of radial and tangential with respect to cell orientation. For a circular cross-section of the stem, the cell orientations at a particular point (x, y) are

indicated in Figure 3. The angle θ is related to position in the stem by

$$\tan\theta = \frac{x}{y} \tag{8}$$

In other words, at any given point (x, y) in the section, the corresponding coordinate system $Ox'y'$ is local and depends on the angle θ according to Eq. (8). In addition, the variables k_l and k_a are renamed k_r and k_t respectively, so as to reflect these radial and tangential orientations.

The following relations (from definitions of the sine and cosine functions along with the Pythagorean theorem) will be useful for substitution into the conductivity tensor:

$$\sin\theta = \frac{x}{\sqrt{x^2+y^2}} \quad \cos\theta = \frac{y}{\sqrt{x^2+y^2}}$$
$$\sin^2\theta = \frac{x^2}{x^2+y^2} \quad \cos^2\theta = \frac{y^2}{x^2+y^2} \tag{9}$$

giving, by substitution into Eq. (7):

$$\underline{K} = \begin{bmatrix} \frac{k_r x^2 + k_t y^2}{x^2+y^2} & \frac{(k_r - k_t)xy}{x^2+y^2} \\ \frac{(k_r - k_t)xy}{x^2+y^2} & \frac{k_t x^2 + k_r y^2}{x^2+y^2} \end{bmatrix} \tag{10}$$

In general, for a 3D Cartesian coordinate system, the conductivity tensor would be of the form

$$\underline{K} = \begin{bmatrix} k_{xx} & k_{xy} & k_{xz} \\ k_{yx} & k_{yy} & k_{yz} \\ k_{zx} & k_{zy} & k_{zz} \end{bmatrix} \tag{11}$$

where, again, the first subscript refers to the direction of flow occurring in response to a force in the direction given by the second subscript. Typically, based on Onsager's principles of irreversible processes (Onsager 1931, Ozis1968), the tensor is symmetrical such that $k_{ij} = k_{ji}$ for $i \neq j$. Also, for the present case where the cells are oriented along the z-axis of the cylinder, $k_{xz}=k_{yz}=k_{zx}=k_{zy}=0$ because a force in the x or y direction has a zero component in the z direction. Therefore, the full tensor for this cylindrical stem would be

$$\underline{K} = \begin{bmatrix} \frac{k_r x^2 + k_t y^2}{x^2+y^2} & \frac{(k_r - k_t)xy}{x^2+y^2} & 0 \\ \frac{(k_r - k_t)xy}{x^2+y^2} & \frac{k_t x^2 + k_r y^2}{x^2+y^2} & 0 \\ 0 & 0 & k_z \end{bmatrix} \tag{12}$$

where k_z is the conductivity along the cylinder axis, parallel to the long axis of the conducting cells. If the orientation of cells permits the alignment of a coordinate system with the arrangement of the cells, the conductivity tensor is further simplified such that $k_{ij} = 0$ for $i \neq j$ (tensor in Eq (12) becomes a diagonal matrix). The symmetrical nature of this tensor has also been described in models of soil water flow (Raats et al. 2004).

The anatomical characteristics of this biological system suggest the use of axial, radial and tangential directions for expressing conductivity (cell faces are oriented in these directions). A coordinate system aligned in these directions would yield a conductivity tensor with non-zero elements only on the diagonal. Similar relationships for the tensor describing conductivity to heat flow in crystalline solids have been developed (Ozisik 1968), where the alignment of the coordinate axes with the crystal structure permits a reduction in the number of non-zero components of the tensor. However, in many circumstances this alignment may not be useful or even possible. For example, in the junction between a stem and its branches, the cell orientations vary with location through the junction, and therefore a conductivity tensor would have to incorporate coordinate system transformations in all three coordinates, leading to non-zero values for all tensor elements.

Application of anisotropy concepts

The models of flow through stems will assume steady-state flow with no water storage (simple conductive medium) and were therefore based on:

$$\nabla \cdot (\underline{K}\nabla P) = 0 \tag{13}$$

where K is the conductivity tensor as described previously, and ∇P is the partial gradient of pressure with respect to the x, y and z directions (MPa m^{-1}), making Eq. (13) a partial differential equation. As a conductive medium lacking storage, Eq. (13) includes a continuity assumption such that water flowing into one region of the flow domain must be balanced by flow out of the region. The numerical solution to this model equation gives P as a function of the spatial variables x, y and z, Flow velocity may be calculated as:

$$J = \underline{K}\nabla P \tag{14}$$

where J is the flow velocity (m s^{-1}) at a point (x, y, z) through the stem. The velocity J at the inlet or outlet may be integrated over the area of the inlet or outlet boundaries to give an estimate of the volumetric flow (m^3 s^{-1}) that may be compared with flows determined experimentally. In addition, dividing this volumetric flow by the applied pressure difference gives an apparent conductance that may be useful for describing the effect of cuts on flow independent of the actual pressure applied. Note that both of the terms 'conductance' and 'conductivity' are used here and in the following sense: conductance is an extrinsic property applicable to a particular instance of a conducting structure such as a plant stem and will have units of m^3 MPa^{-3} s^{-1}. For these units, the basic quantity of water is considered volume; mass or molar quantities can also be used. On the other hand, conductivity is an intrinsic property equivalent to a conduc-

tance per unit length and per unit area, with units of m^2 MPa^{-1} S^{-1} As noted by Schulte and Costa (1996), the term 'per' as used here is often taken to mean 'divided by' but strictly means 'with respect to every member of a group' and is appropriate in this case where conductance is multiplied by length and divided by area.

Methods

Measurement of hydraulic conductance

The hydraulic conductance of the xylem in stems of Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco) was measured with a pressure-flow apparatus comprising a sample stem inserted into tubing and a source of partial vacuum applied to the downstream side of the stem. A glass pipette was located on the upstream side of the sample stem and used for measuring flow rate by timing the progress of a meniscus in the pipette. The pressure difference across the stem through which flow occurred was measured (Omega Engineering HHP-720) as pressure difference between the applied partial vacuum and the atmosphere. Conductance is then calculated from the relation:

$$K = \frac{Q}{\Delta P} \qquad (15)$$

where Q is the measured volumetric flow rate (m^3 s^{-1}) and P is the applied pressure (MPa), giving hydraulic conductance, K (m^3 MPa^{-1} S^{-1}). The flow solution was 20 mM KCl using water de-aired by boiling and undisturbed cooling.

The measured conductance obtained by the pressure-flow method was routinely corrected to a reference temperature of 20°C based on the viscosity of water because small differences in temperature between stem samples would affect flow and hence the conductance estimate. This correction is small but not trivial; for example, the viscosity of water from 20 to 22°C decreases by nearly 5%. Measurements of flow through stems over extended time periods were needed for the repeated conductance measurements associated with gradually deepening cuts to the stem. Preliminary experiments showed that measured conductance did not decline following repeated measurement and further was not affected by the concentration of KCl in the flow medium (data not shown).

Solutions of the mathematical model require estimates of conductivity in the axial, radial and tangential directions. Measurements of conductance through uncut stems provided the axial conductivity. Two sources were used for estimates of radial and tangential conductivity: values from the literature and secondly from a series of measurements made on stems of various conifers while one of the authors (P.J.S.) visited Oregon State University (J.C. Domec, Barbara Lachenbruch and Rick Meinzer). For the latter source, estimates of conductivity were obtained using a high-pressure flow meter (HPFM; homemade version similar to one made by Dynamax Inc., see Tyree et al. 1993, Meinzer et al. 2004) applied to cores of wood (12 mm diameter) cut with an increment corer or a hollow drill bit. Cores were obtained at approximately radial and tangential orientations and then soaked in a vacuum chamber for 2 h to remove air bubbles from the samples. After fitting to the HPFM, pressure was applied and flow rate determined after a steady-state flow was observed. Conductance was calculated as above and conductivity estimated from the measured conductance divided by core cross-sectional area and multiplied by core length. A proper sealing of the core within the pressure fitting of the HPFM was verified by applying safranin stain to the upstream end and observing that tracheids within the core became stained as opposed to only the outer surface of the core becoming stained as was apparent when leaks were present. The HPFM was calibrated by measuring flow rate onto a balance as a function of applied pressure across the capillary tubes used within the instrument for estimating flow (see Tyree et al. 1993 for details). Conductivity values obtained from the literature (Cloutier and Fortin 1993, Tremblay et al. 2000) were expressed in units of kg^2 m^{-1} S^{-1} J^{-1} This measure uses energy per mass units for water potential (J kg^{-1}), which must be converted to the pressure units used here (energy per volume; J m^{-3} = Pa) through multiplying by 1000 J kg^{-1} MPa^{-1}. In addition, the mass unit quantity of water (kg) must be converted to volume using the density of water (998.21 kg m^{-3} at 20°C).

Double sawcut experiments

For experiments on the effect of sawcut depths in the xylem, stems were obtained from 15- to 25-year-old Douglas-fir trees in the Wind River Experimental Forest of the Gifford Pinchot National Forest within the southern Washington Cascade Range (45°49' N, 121°59' W, 560 m elevation). Vertically oriented main stems near the tops of the trees were used to avoid the xylem asymmetry that results from the production of compression wood in non-vertical stems. Tissues exterior to the cambium were removed under water at the ends of the stem segments and at the locations intended for the cuts into the stem to allow for a tight seal into the tubing system. Stems varied in diameter from 10 to 17 mm and from 101 to 160 mm in length. Cuts were located on opposite sides of the stem at approximately one-third and two-thirds of the distance along the stem and were made using a hacksaw blade of approximately 1 mm thickness. The cuts were therefore 30-50 mm apart, much greater than the length of individual tracheids. However, the cuts in the stem would have allowed air to enter tracheids on either side of the cuts, and therefore the region available for lateral flow between the cuts (30-50 mm apart) is likely a few millimeters shortened. Hydraulic conductance was measured as described previously. A repeated series of conductance measurements and cutting followed, giving 8-12 measurements as the cuts progressed until well beyond overlapping. The remaining uninterrupted area for conduction was termed 'clear area' (see Appendix for full expression, available as Supplementary Da-

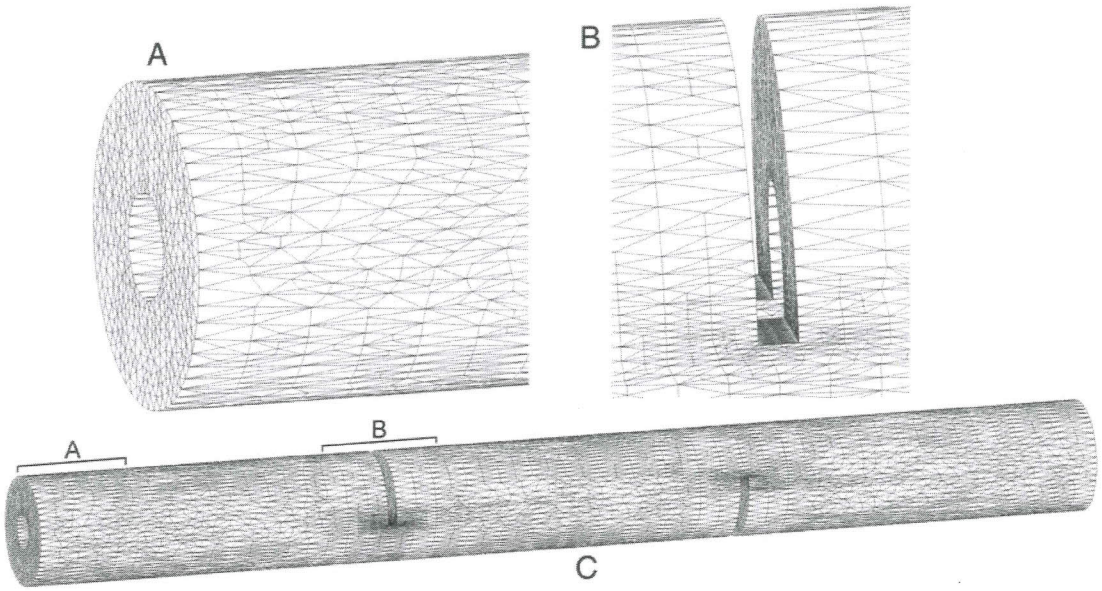

Figure 4. Finite element mesh developed for the 3D model capable of utilizing the anisotropic conductivity tensor. Shown is the full mesh (C), a closer view of the mesh at the inlet (A) and a closer view of the region near one cut (B, cut to 60% depth in this case). Also visible is the open region representing the non-conducting inner stem. Note that mesh density is increased near the cuts, where greater pressure gradients may occur. All boundaries shown were set to a no-flow condition, except the inlet, which was set to a pressure of 0.02 MPa and the outlet, which was set to zero pressure.

ta). Following the last measurement on stems with cuts, a section of the stem upstream from the first cut was removed, and a conductance measurement was made of the intact stem for estimation of axial conductivity. Lastly, a solution of 0.1% safranin stain was passed through this intact stem segment to determine the extent of non-conducting older growth rings and pith. An estimate of tracheid diameter was obtained for use in comparing stem conductivity values with those in the literature. Hand sections were made of the stem xylem and stained briefly in 0.1% safranin. Images of earlywood from the outer two growth rings of these sections were analyzed with the ImageJ program *(http://rsb.info.nih.gov/ijl)* for measurement of tracheid diameter. Conductivity is not linearly related to tracheid diameter, and so, following the Hagen-Poiseuille relation (Zimmermann 1983), tracheid diameter was weighted by its fourth power in calculating an average diameter.

Model solutions

Models were developed of the stem with cuts using the Comsol Multiphysics software *(http://www.comsol.com)*. a general partial differential equation (PDE) solver. This program includes facilities for developing the system geometry using a 3D computer-aided-design (CAD) process, discretizing the model PDE as expressed in Eq. (13) over the geometry to produce a finite element mesh and solving this model. The model geometry (Figure 4) was based on a representative stem of Douglas-fir with a diameter of 12 mm and a pith diameter of 4 mm. The non-conducting pith region represented a combination of the actual stem pith along with the inner non-conducting primary xylem, metaxylem and non-functional inner rings of secondary xylem, regions that did not stain during the staining process following experimental treatments. Boundary conditions at the inlet and outlet faces of the cylinder reflected applied pressures of 20 and 0 kPa, respectively. Models were developed with 1 mm thick conducting regions removed (representing the cuts in the stem) at depths of 10-90% of the stem diameter (50% meaning the cuts just reach the center of the stem). Values for the parameters k_r and k_t were based on two sources as noted previously: experimental measures of conductivity with cylinders of wood cut in the radial and tangential directions and values in the literature obtained from studies of drying lumber (Cloutier and Fortin 1993, Tremblay et al. 2000). Values for the parameter k_z were based on the measured conductance of stems without cuts (lateral flow would not in principle be a factor in this case because the pressure gradient is applied only in the axial direction).

Results

The nine stems utilized for application of double cuts varied in diameter, and therefore to express the effect of cuts on conductance in common for all samples, both conductance and clear area (see Appendix) were normalized by dividing by maximum values for each variable. For reference, the actual conductances (unnormalized) of the uncut stems varied from 3.1 E-07 to 1.9 E-06 $m^3\ MPa^{-1}\ s^{-1}$. Conductance for each sample stem began declining rapidly as the cut depth in-

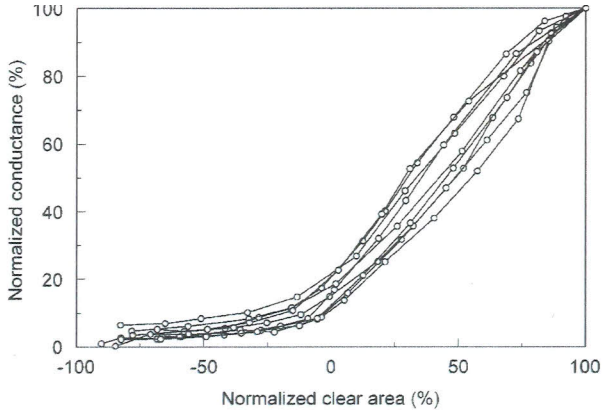

Figure 5. Experimental results showing the effect of double cuts to the Douglas-fir stems. Hydraulic conductance (normalized by the maximum conductance prior to the first cuts) is shown as a function of the calculated clear area for flow (normalized by the stem area, minus pith, prior to cutting). Each line represents one of nine individual stems for which conductance was measured with increasing cut depth. Clear areas less than zero reflect overlapping cuts.

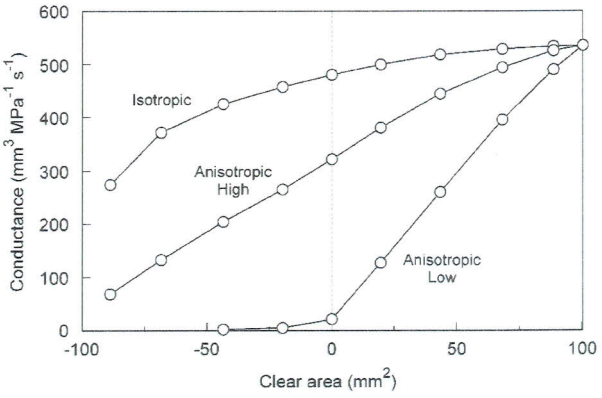

Figure 6. Model results from simulations of stems with cuts of various depths, showing flow as a function of clear area for conduction. Clear area is the area of the cross-section that would be available for flow in the axial direction throughout the length of the stem. Cuts to the center of the stem give a clear area of zero, and for overlapping cuts to greater depth, the clear area is negative (see Appendix A for further detail). Model results are labeled 'Isotropic' for models with $k_r = k_t = k_z = 638.66$ mm^2 MPa^{-1} s^{-1}, 'Anisotropic High' for models with $k_r = 2.292$, $k_t = 18.502$, $k_z = 638.66$ mm^2 MPa^{-1} s^{-1} and 'Anisotropic Low' for models with $k_r = 0.03$, $k_t = 0.03$, $k_z = 638.66$ mm^2 MPa^{-1} s^{-1}.

creased (Figure 5) until the cuts overlapped (clear area <0), after which the conductance declined more gradually. For the nine samples, conductance with a clear area of zero (cuts 50% through the stem) ranged from 11% to 23% of the uncut value. Strongly overlapping cuts still yielded flow despite the obvious lack of a clear path through the stem. For example, a normalized clear area of -75% in Figure 5 corresponds to a 12-mm-diameter stem with a 4-mm-diameter non-conducting region whereby each cut extends to a depth of 10.54 mm, and yet conductance was still roughly 5% of the initial, uncut stem value.

Estimates of radial, tangential and axial conductivity from measurements by the authors and from values in the literature show considerable variation (Table 1). In general, radial and tangential conductivity was two to three orders of magnitude lower than axial conductivity. The values for k_r and k_t from Cloutier and Fortin (1993) and Tremblay et al. (2000), although from conifers but not *P. menziesii* as used in the present work, are roughly two orders of magnitude lower than measured by the authors.

For the trivial case of an uncut stem, model solutions closely match experimental results. For example, an experimental stem of 12.1 mm diameter and 159.6 mm length, with a non-conducting pith region of 3.1 mm diameter and under an applied pressure of 0.0184 MPa, produced a measured flow of 8.576 mm^3 s^{-1}. Corrected to a reference temperature of 20°C (because of the small change in the viscosity of water at the stem temperature of 21°C), this measurement yielded an axial conductivity estimate for that stem of 675.73 mm^2 MPa^{-1} S^{-1}. A model of these dimensions and conductivity predicted a

Table 1. Radial, tangential and axial conductivities used in stem models. The conductivity values labeled 'HPFM' (derived from the high-pressure flow meter measurements) were used in models referred to as the 'Anisotropy High' case, whereas values for radial and tangential conductivity derived from the literature were used in the 'Anisotropy Low' case.

	Conductivity (mm^2 MPa^{-1} s^{-1}) source	
Direction	HPFM[a]	Literature[c]
Radial	2.292	0.035[d]
Tangential	18.502	0.028[d]
Axial	500.05 638.66[b]	100.0[e]

[a]Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco).
[b]Value obtained from measurements with stems used in experiments where cuts were applied.
[c]Cloutier and Fortin 1993; Tremblay et al. 2000.
[d]Red pine (*Pinus resinosa* Aiton) sapwood.
[e]Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.).

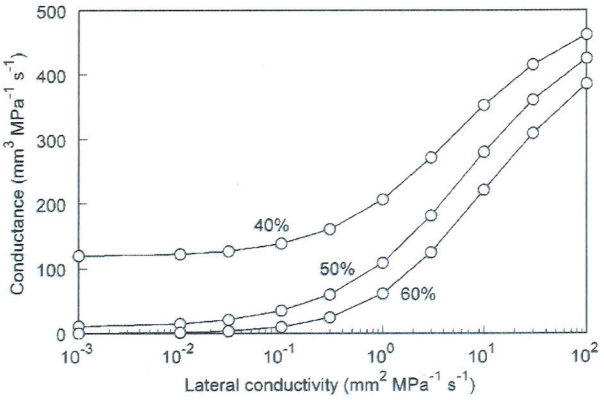

Figure 7. Conductance to flow through stems simulated by the 3D model, with cuts at the three depths indicated, as a function of the lateral conductivity ($k_r = k_t$).

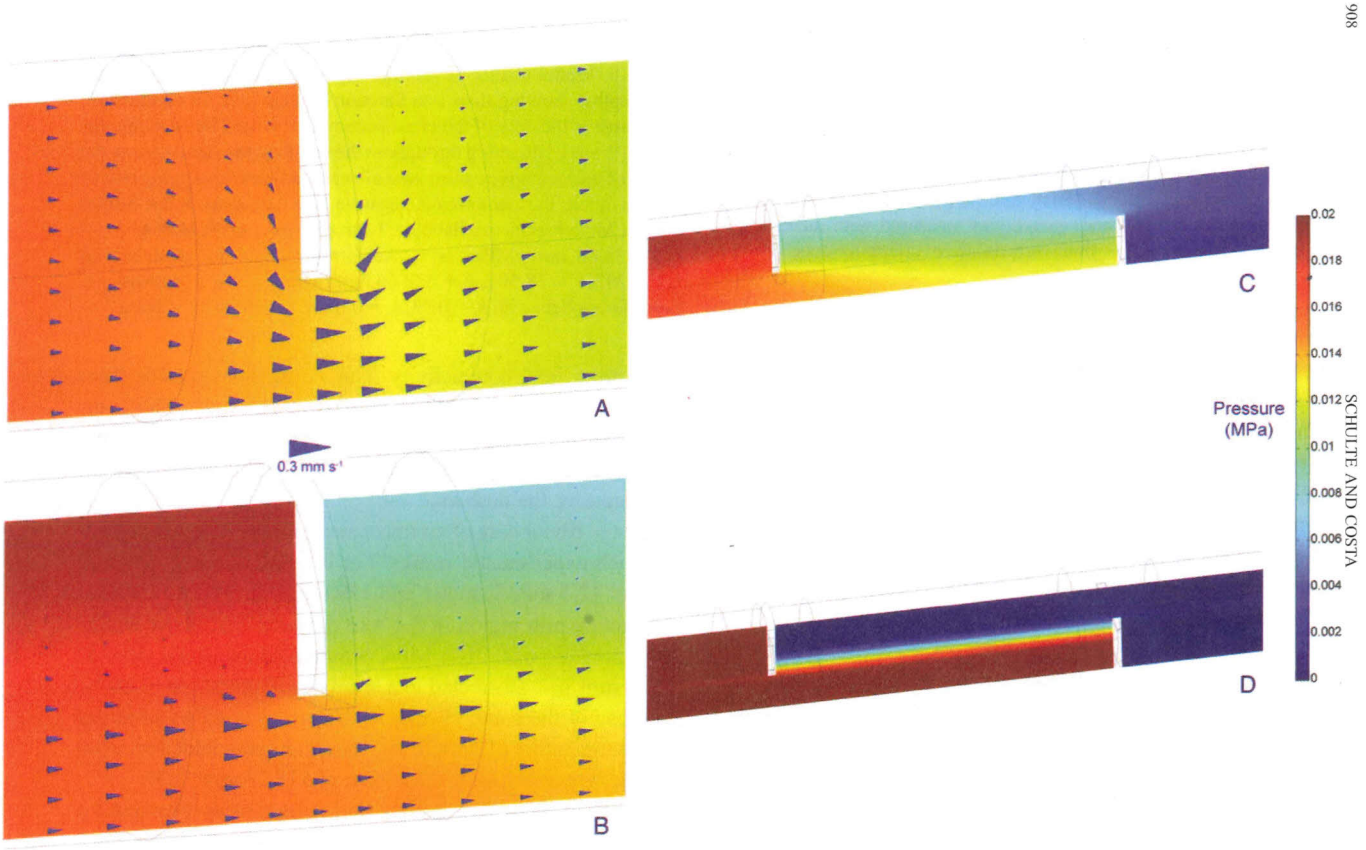

Figure 8. 3D model solutions for the stem with cuts to 60% depth. (A) Pressure (scale at right) and flow (arrows) near the upstream cut for the model with isotropic conductivity ($k_r = k_t = k_z$ = 638.66 mm^2 MPa^{-1} s^{-1}). (B) Pressure (scale at right) and flow (arrows) near the upstream cut for the model with high anisotropic conductivity (k_r = 2.292, k_t = 18.502, k_z = 638.66 mm^2 MPa^{-1} s^{-1}). (C) Pressure (scale at right) for the central region of the model with high anisotropic conductivity (k_r = 2.292, k_t = 18.502, k_z = 638.66 mm^2 MPa^{-1} s^{-1}). (D) Pressure (scale at right) for the central region of the model with low anisotropic conductivity (k_r = 0.03, k_t = 0.03, k_z = 638.66 mm^2 MPa^{-1} s^{-1}). This figure appears in color in the online version of *Tree Physiology*.

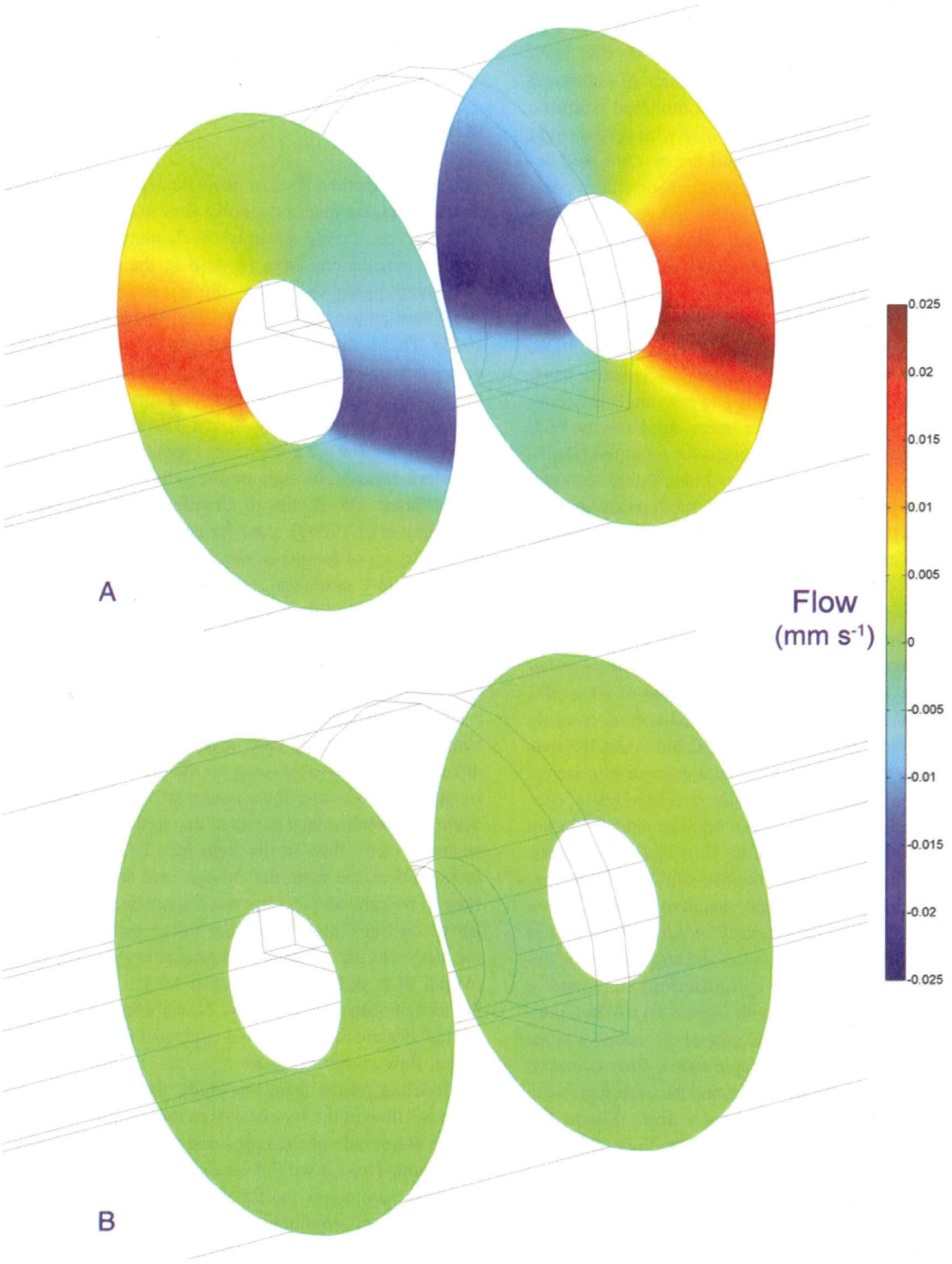

Figure 9. Flow velocities (mm s^{-1}) from the 3D model with cuts to 60% depth on a planar surface 5 mm before and after the upstream cut in the stem. (A) Tangential velocity, where positive values indicate flow in the counter-clockwise direction. (B) Radial velocity, where positive values reflect flow outward radially from the center. This figure appears in color in the online version of *Tree Physiology*.

flow of 8.5747 mm^3s^{-1}; within 0.015% of that measured. The same experimental stem was also used for obtaining an estimate of tracheid diameter (fourth power weighted mean), yielding a mean diameter of 23.0 um (SD = 2.4 um, n = 134). This information was not used in the experimental measures or models of stems with double cuts but for later comparison of measured axial conductivity with literature values.

For models with cuts in the stem, estimates of whole stem conductance from the 3D model declined as cut depth increased but depended strongly on the values of radial and tangential conductivity (Figure 6). The modeled isotropic stem ($k_r = k_t = k_z$) shows high conductance with only a slight decline as the cut depth increased until the cuts are well beyond overlapping. The effect of cuts in anisotropic models depended on the applied values of radial and tangential conductivity, using either the relatively high values from the author's measurements or the lower values obtained from the literature. For 50% cut depth (clear area of zero), conductance was reduced to 60% of uncut conductance for the high conductivities and to 4% for the low conductivities. For cuts of 90% depth, conductance was 13% of the uncut conductance using the high values of lateral conductivity and essentially zero conductance based on the low values for lateral conductivity. With regard to the numerical solution process for these models, finite element size was varied, yielding about 50,000-400,000 elements, and these changes to the model mesh produced only minor changes in the flow rate through the model. The similarity of model solutions as finite element size was reduced (greater number of elements) suggests that an adequate finite element density was employed to represent the overall flow regime within the model.

The effects of radial and tangential conductivity were examined more closely for 3D models with cut depths of 40%, 50% and 60% (Figure 7). Conductance declined with decreasing lateral conductivity for all three models, but when the cuts did not overlap as in the 40% model, conductance approached a value of 120 mm^3 MPa^{-1} s^{-1}. Even for zero lateral flow, conduction would still occur in this case because the cuts do not overlap and there is still clear area for flow between the cuts. When cuts just met (50%) or overlapped slightly (60%), conductance approached zero as lateral conductivity declined.

The 3D models show that lateral flow around the cuts is strongly obstructed by the small radial and tangential conductivity relative to axial conductivity (anisotropy) as found in stems (Figure 8B as compared with Figure 8A). When conducting ability in the radial and tangential directions was set equal to axial conductivity (isotropic case), flow occurred readily around the narrow (1 mm) cuts, and the overall pressure gradient along the axis of the stem was uniform (Figure 8A, steady pressure drop along the cell axis). On the other hand, for the anisotropic cases (Figure 8C and D), the pressure drop becomes focused into the region between the cuts. This is particularly apparent in the anisotropic, low conductivity case (Figure 8D), where the pressure drop is almost entirely within the region of cut overlap. Note also that the pressure gradient is oriented in the lateral direction, where conductivity is much lower than axially. Model results also suggest that the flow pathway in the vicinity of the cuts is dominated by tangential rather than radial flow (Figure 9). Flow before the cut is primarily tangential: peak tangential flow velocity is 12-fold greater than peak radial flow velocity. A sensitivity analysis of flow to changes in radial and tangential conductivity (not shown) also indicated that for all values of both parameters, flow is more sensitive to tangential conductivity than to radial conductivity.

Discussion

The present mathematical models demonstrate the manner in which lateral conductivity allows flow along the stem despite the presence of even strongly overlapping cuts to the stem. Similar conclusions were reached in the early experiments with overlapping sawcuts to the stems of trees (Greenidge 1955, Postlethwait and Rogers 1955, MacKay and Weatherly 1973). The declining stem conductance in the face of deepening cuts observed experimentally here falls in between model results based on the high and low values utilized for radial and tangential conductivity. The slope of the conductance decline (or the conductance remaining with 50% cuts) therefore depends strongly on the values used in the conductivity tensor. The studies of Cloutier and Fortin (1993) and Tremblay et al. (2000) cited for conductivity values focused on the drying of lumber at moisture contents from saturation to well below saturation, but data for saturated wood were utilized herein and thus should be relevant for functional xylem in living plants. The cuts made to experimental stems would have allowed air to enter open tracheids, and so the region for lateral flow would be slightly reduced in length, a situation that might need to be considered for models of vessel-bearing species. One might also note that the pressure difference applied to the stem for the present experiments and models was the same for all cut depths, and so flow would decline as conductance declined due to the cuts. Of course in an intact plant, flow in the stem may be determined by the transpiration rate from the foliage, and so it is possible for flow to be maintained if the water potential of the transpiring leaves declines, thus increasing the pressure gradient along the stem. On the other hand, stomatal responses may reduce overall flow and limit changes in foliage water potential in the face of obstructions to flow. Nonetheless, the continuation of flow despite the obstructing cuts must depend on increased lateral flow within the stem.

Modeling results from this study suggest that the maintenance of flow in the face of cuts to the stem depends strongly on the magnitude of the radial and tangential conductivity of the xylem. Thus, it will be crucial to have appropriate values for these parameters for future studies where flow may depend on lateral conductivity. Conductivity measured in the present work varied over a twofold range between samples, perhaps because the exact orientation of the sampled core is critical and even more so in comparison with literature-derived values. Experimental measurements of radial and tangential conductivity with the HPFM might be higher than experienced by the stems used for double-cut experiments here because the conductivity measurements were made on saturated stems, whereas the sample stems for double-cut experiments contained non-functional xylem as indicated by staining patterns (not shown). Radial conductivity values

from Douglas-fir sapwood as shown by Domec et al. (2005) of 1.3-1.8 mm^2 MPa^{-1} s^{-1} (converted from their units of kg m^{-1} MPa^{-1} s^{-1}) are somewhat similar to our value of 2.9 mm^2 MPa^{-1} s^{-1}. Axial conductivity reported by Domec et al. (2005) was approximately 2000-fold greater than radial conductivity, an even greater ratio than observed here. In addition, axial conductivity from their xylem samples was four- to fivefold greater than axial conductivity as reported here, possibly because the tracheids in their outer sapwood samples were of greater diameter (31.8 vs 23.0 um as measured for outer growth rings here). Scaled to the fourth power, this difference would account for a 3.7- fold difference in conductivity. Domec et al. (2005) estimated that radial tension gradients in the xylem were considerably greater than axial gradients, but flow in the radial direction was limited by the much lower conductivity in that direction as compared with conductivity in the axial direction. Similarly, our results indicate that large lateral pressure gradients may develop in the xylem in association with obstructions such as cuts, but flow is limited by the low conductivity in that direction.

Results from this study also suggest that tangential flow is more significant for flow around the cuts than radial flow, likely due in part to the presence of a non-conducting pith region of the stem. Tangential conductivity may be higher than radial given anatomical considerations (pits almost exclusively on radial walls; Siau 1971, Panshin and de Zeeuw 1980). The dominance of tangential flow around the cuts is therefore dependent upon a combination of having tangential conductivity greater than radial conductivity along with the presence of the pith and other non-conducting regions at the center of the stem xylem. The significance of tangential flow may also apply to naturally occurring obstructions or other deviations from a simple cylindrical stem. Previous studies of flow through branch junctions in stems and roots also demonstrated the importance of tangential flow based on staining patterns observed during flow between branches (Schulte and Brooks 2003, Schulte 2006). In an evolutionary sense, it is interesting to speculate that a stem may be well-interconnected laterally with a radial conductivity much less than the tangential conductivity. Such a scenario appears to correspond with xylem tissue anatomy whereby pits occur primarily along radial walls of tracheids thus favoring lateral flow in the tangential direction. On the other hand, more pits on tangential walls would increase radial conductivity but perhaps not lead to greater lateral flow because of the presence of non-conducting pith, primary xylem and early growth rings. Therefore, the observed distribution oftracheid pits appears to correspond with provision for lateral flow.

Radial conductivity in the xylem of conifers has been reported as greater than tangential conductivity (Cloutier and Fortin 1993, Defo et al. 1999), and it was suggested that flow through xylem rays may account for the observed differences. This result contrasts with our measures of radial conductivity as less than tangential conductivity, which could be accounted for by greater pit density on radial walls of the tracheids (allowing flow tangentially) as compared with tangential walls. Given the presence of a non-conducting region at the stem center, it is not clear how radial flow would contribute to flow across the entire stem, although more localized flow may be enhanced. Further work is clearly needed to describe these important parameters governing lateral flow in the xylem. For measurements of radial and tangential conductivity, careful attention to orientation of the sample will be important. For example, if conductivity along the axis of the tracheids is two or more orders of magnitude greater than radial and tangential conductivity, slight errors in the orientation of the sample during measurement would create large errors in the conductivity estimate because of the resulting contribution of axial flow. As an additional consideration for further development, xylem conductivity would be expected to depend on the embolism of conduits due to cavitation (Hacke et al. 2005). Although conductivity in lateral as well as axial directions might be affected by the occurrence of cavitation-derived embolism in tracheids, hypothetically, lateral conductivity may be affected to a greater extent. The embolism of half of the tracheids observed in a cross-section of stem might halve axial conductivity but even more strongly impact lateral flow if these embolisms were to isolate groups of tracheids, equivalent to a sectorialized xylem. Such isolated groups of tracheids could still allow some axial flow but would be prevented from exchanging with other groups because of the blocked lateral connections. Thus, we suspect that the dynamic nature of xylem disruption by embolism may be particularly significant for lateral flow.

Xylem anisotropy is important in both physiological and ecological contexts. Taneda and Tateno (2007) considered models of shoots supplying leaves through either interconnected or independent pathways for kudzu vines. The interconnected model was a better fit to the observed distribution of conductivity and reflected the need for vessel-to-vessel contact to allow for lateral flow across stems. A few studies have considered the role of lateral transport capability on whole plant water relations. Ellmore et al. (2006) applied a dye transport method along with hydraulic measurements to three species of temperate hardwoods to classify them along a continuum from integrated to sectored. The authors suggest that the degree of integration is directly related to relative differences in axial and lateral resistance (inverse conductance) to flow. If lateral resistance is low enough, flow can occur readily across the stem, and such a stem might be termed integrated. Highly integrated species have anatomical characteristics such as high intervessel pitting density and proximity of individual vessels contributing to their integrated nature (Orians et al. 2004). In a study of shrubs across an aridity gradient, Schenk et al. (2008) discuss the role of hydraulic integration within stems. Hydraulic integration proved advantageous in humid environments, whereas modularity (sectoriality) was more common in aridland shrubs. While integration would allow for flow around obstructions, modularity would protect parts of the shrub while segmenting or isolating parts having lost their transport connections. A study of an addi-

tional 18 species of woody trees and shrubs (Zanne et al. 2006) based on anatomical characteristics of xylem vessels provided further support for the idea that sectored species would have an advantage in xeric environments. Sectoriality may be important for plant-herbivore interactions by affecting the heterogeneity of resources for herbivores within a plant canopy (Orians and Jones 2001). Therefore, the above studies demonstrate the importance of lateral flow capability in woody plants both for transport and distribution of materials within the whole organism and for the occurrence of species in various environments.

The mathematical approach to transport incorporating anisotropy will be useful for more complex geometries beyond artificial cuts to the stem, and herein will lie its true usefulness. But the application of this approach will depend on reasonable values for radial and tangential conductivity. Given the sensitivity of flow to lateral conducting ability where artificial obstructions such as cuts are present, it will also be important to enhance our understanding of how these variables change with embolism of vascular conduits. As recent papers have suggested (Domec et al. 2007), xylem conductivity may vary as a function of flow through tracheids, perhaps as a result of dynamic changes in pit membrane structure. Such considerations can be applied to the conductivity tensor, making the conductivity components a function of dependent variables (like pressure or flow velocity), thus introducing a non-linearity to the basic partial differential equation (Eq. (13)), which could be readily incorporated into future work. Future work will also extend this approach to anisotropy of xylem conductivity into naturally occurring stem features such as junctions, where the interaction between component branches depends on lateral flow (Schulte and Brooks 2003, Schulte 2006). Within such junctions, the axial, radial and tangential orientations of the tracheids will vary spatially (see for example Kramer and Borkowski 2004), and so these orientation changes will have to be incorporated through coordinate transformations into all of the off-diagonal components of the conductivity tensor. Once expressed, this approach, although leading to a more complex tensor, should create no additional difficulties by way of numerical solution of the transport equations.

Supplementary Data

Supplementary data for this article are available at *Tree Physiology* Online.

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