

How does a gymnosperm branch (*Pseudotsuga menziesii*) assume the hydraulic status of a main stem when it takes over as leader?

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ABSTRACT

In most gymnosperms, resistance to the flow of water per unit path length through the main stem is less than that of lateral branches. Using branches, leaders, and branches that have replaced missing leaders ('branch-leaders'), we tested the hypothesis that branch-leaders are at a hydraulic disadvantage. Reduced xylem transport efficiency in branch-leaders relative to leaders could be expected both because of an initial disparity in hydraulic capacity, and because of the relatively impermeable compression wood formed in branch-leaders during shoot reorientation. By subsampling branch-leaders, we also tested the hypothesis that opposite wood (formed directly opposite compression wood) is more permeable than normal wood, and could, therefore, compensate for the presence of compression wood at the whole shoot level. Fifteen months after leader removal, branch-leaders were intermediate between branches and leaders in their ability to supply foliage with water, suggesting a transition towards leader status that was not yet complete. Increased hydraulic capacity in branch-leaders was the result of increased xylem cross-sectional area per unit foliage, rather than an increase in permeability. Among subsampled wood types from basal branch-leader segments, opposite wood was significantly less permeable than normal wood, suggesting that it does not compensate for the presence of compression wood.

Key-words: *Pseudotsuga menziesii*; compression wood; hydraulic conductivity; leaf-specific conductivity; opposite wood; specific conductivity; xylem structure.

INTRODUCTION

The top of a tree must receive an adequate supply of water for the tree to grow in height and compete successfully for light in a forest setting. This is achieved, in part, through patterns of variation in xylem anatomy and geometry that create a hierarchy of resistance to the flow of water through a single stem. Numerous studies on plant hydraulic architecture have established that the resistance to flow (per unit path length) in the main stem is less than that in first order

branches, and similarly, that the resistance to flow (per unit path length) is less in first order than in second order branches (Zimmermann 1978; Tyree *et al.* 1983; Ewers & Zimmermann 1984a,b; Sellin 1987). This pattern of resistances allows branches at the top of a tree to compete successfully for water with those lower in the crown, and also reduces the risk of injury (i.e. loss of conductive capacity due to cavitation) to the main stem during drought. The enhanced supply of water to the leader is often considered a hydraulic expression of apical control that allows the leader to have greater elongation growth than lateral branches (Ewers & Zimmermann 1984a; Sellin 1987). Indeed, in species that lack strong apical control (i.e. species in which the leader is frequently replaced by a lateral), there is little difference in hydraulic capacity between the leader and adjacent laterals (Farmer 1918; Ewers & Zimmermann 1984b).

The replacement of a damaged or missing leader by a lateral branch is a common occurrence in gymnosperms and requires the action of compression wood in the replacement axis (Sinnott 1952; Wilson 1973; Wilson & Archer 1981; Wilson 1986). Does the branch assume the favoured hydraulic status of the main stem, or is the new leader put at a hydraulic disadvantage because of its origin as a branch? If the branch *does* assume the hydraulic status of a leader, does it do so through an increase in xylem permeability, an increase in transverse conducting area, or a combination of both? The questions posed are interesting, not only because of the initial hydraulic disparity between branches and leaders, but also because of the large amount of relatively impermeable compression wood (Spicer & Gartner in press) that must form in branches that take over as leaders. Some studies suggest that the wood formed opposite compression wood ('opposite wood') has anatomical characteristics opposite those of compression wood, and that only the wood formed to the sides ('lateral wood') can be considered normal (Timell 1973; Park 1983, 1984a,b; Lee & Eom 1988). Do the hydraulic properties of opposite wood make up for lost conductive capacity due to compression wood? Although we know of no study aimed at answering these questions, one set of preliminary observations suggests that the hydraulic status of a branch *does* improve during the transition to leader, largely as a result of increased transverse conducting area (Ewers & Zimmermann 1984a).

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In the current study, we explored answers to the questions listed above by studying the hydraulic properties of shoots in young Douglas-fir trees from which we had removed the leader 15 months before, allowing a branch to move up in its place. By comparing the hydraulic properties of 'branch-leaders' with those of intact leaders and branches, we can describe the hydraulic transition from branch to leader. Specifically, we used 1- and 3-year-old shoot segments to test the hypothesis that branch-leaders remain at a hydraulic disadvantage, as quantified by their ability to supply foliage with water. One-year-old branch-leader xylem, formed entirely in the absence of a leader, is expected to have hydraulic properties identical to those of leaders. In contrast, 3-year-old branch-leader xylem, which contains both a 2-year-old core of branch wood and a large amount of compression wood, is expected to have a lower hydraulic capacity than that of leader xylem. Finally, using a new technique to measure flow rates on segments excised from whole stems, we examined the potential for xylem anatomy at the whole shoot level to compensate for the reduced permeability of compression wood by testing the hypothesis that the hydraulic capacity of opposite wood is enhanced relative to that of normal wood.

MATERIALS AND METHODS

Plant material

Fifteen open-grown Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) trees, ranging in age from 5 to 10 years, were selected randomly from a population of about 100 trees. Each tree was then paired with another tree of the same age and similar size selected from the same population. The trees were naturally regenerated and growing in an open field adjacent to Peavy Arboretum at the Oregon State University McDonald Research Forest (44°39'34" latitude, 123°14'01" longitude, 136 m elevation), 10 km north of Corvallis, Oregon, USA. In June 1995, the leader of one tree (selected at random) within each pair was removed just above the second (2-year-old) branch-whorl. The remaining tree in each pair served as a control. By August 1996, one or more lateral branches ('branch-leaders'), then 3 years old, had grown vertically in place of the removed leader for all 15 trees.

Branch-leaders from treated trees and branches and leaders from control trees were harvested from mid-August to early September 1996 for conductivity measurements. The entire 3-year-old branch-leader was removed from each treated tree just above the point of attachment with the main stem. In cases where several branches appeared to be 'competing' for the role of leader, the branch that was most clearly dominant (i.e. longer and more vertical) was removed. From each control tree, the most vigorous 3-year-old branch was removed just distal to the point of attachment with the main stem. The leader of each control tree was then removed just above the third (3-year-old) branch-whorl. Whole branches and stem segments were

removed with loppers and immediately placed in water for transport to the laboratory. All stem and branch material was harvested before dawn to minimize tension in the xylem and decrease the risk of introducing emboli. Shoots from paired trees were always harvested the same day, and all conductivity measurements were made on the day of harvest.

Whole shoot segments

Sample preparation

While immersed in water, segments \approx 5 cm long were excised near the base of both the 1- and 3-year-old portions of the shoot for each branch, branch-leader and leader. The bark was removed from each sample and the ends were trimmed with a razor blade. Sample length, diameter and diameter of the pith were measured with calipers. Most 3-year-old branch-leader segments had significant taper, in which case sample and pith diameters were taken as the average of the distal and proximal ends. Samples were stored in water at room temperature until conductivity measurements were made.

Leaf area

Foliage attached to and distal to each segment was collected to determine leaf dry mass, and subsampled to determine fresh area/dry mass conversions. Based on a visual assessment, appreciable differences in conversion factors based on foliage age and/or position were expected and the following five classes were created: terminal shoot foliage for leader and branch-leader segments; terminal shoot foliage for branch segments; current-year lateral shoot foliage for leader and branch-leader segments; 2- and 3-year-old lateral shoot foliage for leader and branch-leader segments; all ages of lateral shoot foliage for branch segments. For each segment and foliar class, fresh needles were removed from five randomly selected, 4 cm long sprigs. The remaining foliage was dried in an oven for 48 h at 60 °C and weighed. The projected area of fresh foliage samples was determined using a video camera and NIH Image version 1.52 (public domain software developed by the National Institute of Health) on a Quadra 800 Macintosh. The samples were then dried and weighed to establish fresh area to dry mass ratios. Conversion ratios were used to calculate the fresh leaf area distal to each segment for use in leaf-specific conductivity calculations (see below).

Volume flow rate

Flexible tubing was stretched over both ends of whole segments and a dilute solution of oxalic acid (10 mol m⁻³, filtered to 0.22 μ m) was delivered to the distal end under a gravitational pressure head of 0.005 MPa. Oxalic acid has been shown to prevent the decline in conductivity with time that is commonly observed during long measurement periods using distilled water (Sperry, Donnelly & Tyree

1988). Fluid was collected from the proximal end for repeated periods of 1 min and weighed on an electronic balance. The volume flow rate was calculated as the mean of at least five collection periods. To correct for changes in viscosity, thermocouples were used to record the temperature of both the permeating fluid and the water in which the samples were stored.

Specific conductivity

Under a given pressure head, volume flow rate is a function of sample length, cross-sectional area, and conductive efficiency (i.e. permeability). It is, therefore, useful to consider several forms of conductivity. Specific conductivity (k_s) describes the permeability of a sample and is defined by Darcy's law as

$$k_s = Q/lA_s\Delta P \quad (1)$$

where k_s is in $\text{m}^2 \text{s}^{-1} \text{MPa}^{-1}$, Q is the volume flow rate ($\text{m}^3 \text{s}^{-1}$), l is the length of the segment (m), A_s is the sapwood cross-sectional area (m^2), and ΔP is the pressure difference between the two ends of the segment (MPa). Note that *specific* in this instance means *area-specific*, or divided by area, rather than the accepted SI meaning, divided by mass. Similarly, leaf-specific conductivity (defined below) refers to conductivity divided by leaf *area*, not mass. All conductivity calculations were corrected to 20 °C to account for changes in fluid viscosity with temperature.

Hydraulic conductivity

Hydraulic conductivity (k_h) expresses the volume flow–pressure relationship on a length but not area basis, and is defined as

$$k_h = Q/l\Delta P \quad (2)$$

where k_h is in $\text{m}^4 \text{s}^{-1} \text{MPa}^{-1}$ and all terms are defined as above for k_s .

Leaf-specific conductivity and Huber value

Leaf-specific conductivity (k_l) expresses conductivity per distal leaf area rather than per sapwood cross-sectional area and is defined as

$$k_l = Q/lA_l\Delta P \quad (3)$$

where k_l is in $\text{m}^2 \text{s}^{-1} \text{MPa}^{-1}$, A_l is defined as the sum of the projected leaf area both attached and distal to the segment (m^2), and all terms are defined as above for k_s . Huber value (H) is defined as the ratio of xylem cross-sectional area to distal leaf area, and is therefore unitless. Note that

$$k_l = H \times k_s \quad (4)$$

Following conductivity measurements, whole segments (excluding 3-year-old branch-leader segments, which were subsampled, see below) were perfused with filtered (0.22 μm) 0.5% (w/v) safranin-O for 20 min. The earlywood always stained completely, giving no evidence of cavitation.

Branch-leader subsamples: compression, opposite and lateral woods

Sample preparation

Three-year-old branch-leader segments contained large amounts of compression wood and were split longitudinally along their radii (through the pith) for further conductivity measurements. Preliminary tests showed that measuring the volume flow rate twice on the same sample, with several hours between measurements, did not significantly affect the results. Three sectors were drawn with pencil on the distal end of each branch-leader segment, outlining three subsamples, one each from the regions of compression, opposite and lateral wood (Fig. 1). The largest possible sector was drawn within each region to maximize the subsample cross-sectional area and minimize the damage caused by splitting (Spicer & Gartner, in press). With the whole segment immersed in water, a razor blade was used to score the distal end along the pencil lines. A chisel was then slowly forced into each score to split out wedge-shaped subsamples, three per branch-leader segment (Fig. 1).

Subsamples were sealed inside a pressure-sleeve apparatus (described below) for measurements of volume flow rate. Specific conductivity (k_s), as defined above for whole shoot segments, was calculated for each subsample. The cross-sectional area (A , mm^2) of each subsample was equivalent to a sector and calculated as

$$A = r^2\alpha/2 \quad (5)$$

where r is the radius (mm) and α is the central angle in radians. The mean of r and α for the distal and proximal ends of each subsample were used.

Pressure-sleeve apparatus

Samples were kept wet prior to volume flow rate measurements, and as a result, the split radial surfaces could not be sealed with adhesives. Instead, subsamples were enclosed in a modified pressure-sleeve apparatus (Spicer & Gartner in

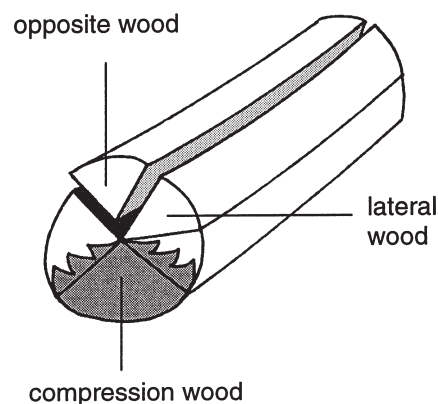


Figure 1. Location of opposite, lateral and compression wood subsamples within 3-year-old branch-leader segments.

press) during conductivity measurements in order to seal the sides of the samples (Fig. 2). A polyvinyl chloride (PVC) coupling device was fitted with a valve from a bicycle tube tyre by inserting the valve through a hole drilled in the wall of the coupling device and sealing it in place with silicone sealer. Clear, 3 mm thick Plexiglass disks, 5 cm in diameter, were cut to fit inside each end of the coupling device. A 5 mm diameter hole was drilled in the centre of each disk to allow connector tubes to pass through either end. Latex sleeves were made from non-lubricated, latex condoms by removing the closed end with a razor blade and wrapping each end around the rubber gaskets of the coupling device.

Subsamples were fitted at either end with connectors made of thick-walled latex tubing, smaller diameter thin-walled tubing, and 5 cm long sections of rigid plastic tubing (Fig. 2). With the subsample inside the latex sleeve, an airtight seal was formed between the sleeve and the rubber gasket by closing the ends of the coupling device. The air inside the chamber was pressurized using a bicycle pump, forcing the sleeve against the sides of the wedge-shaped subsamples to prevent fluid leakage. The splitting process occasionally produced subsamples with irregular radial surfaces. In these cases, we improved the seal by applying a thick layer of silicon vacuum grease to the radial walls of the subsample.

Following a slow air pressurization of the coupling device chamber, the connectors at either end of the subsample were flushed with filtered oxalic acid (see above) to remove air bubbles. Connectors were then attached to the reservoir of oxalic acid (distal end), and to a 1 cm³ graduated pipette (proximal end). Volume flow rates were measured under the same conditions described for whole

segments by timing the movement of the meniscus across 0.1 cm³ intervals. The mean of at least eight timed intervals was used to calculate k_s .

Following the conductivity measurements, the subsamples were perfused with filtered (0.22 µm), 0.5% (w/v) safranin-O under a 0.01 MPa pressure head for 15 min while still enclosed in the pressure-sleeve apparatus. The earlywood always stained completely, giving no evidence of cavitation.

Statistical analysis

A univariate repeated measures analysis was performed using a mixed model to compare same-age segments among shoot types (branch, leader, branch-leader) and different ages (1 and 3 years) within each shoot type. Repeated measures analysis was used to account for correlation between two ages within the same shoot. Multiple comparison adjustments for the *P* values were made using the Tukey–Kramer method. Differences between any two wood types (compression, opposite and lateral wood) subsampled from 3-year-old branch-leader segments were tested with paired *t*-tests. All statistical procedures were conducted with Statistical Analysis Systems software (SAS 1996).

RESULTS

Whole shoot segments

Within each shoot type, 1-year-old segments had lower k_h but higher k_l and *H* than 3-year-old segments (Table 1).

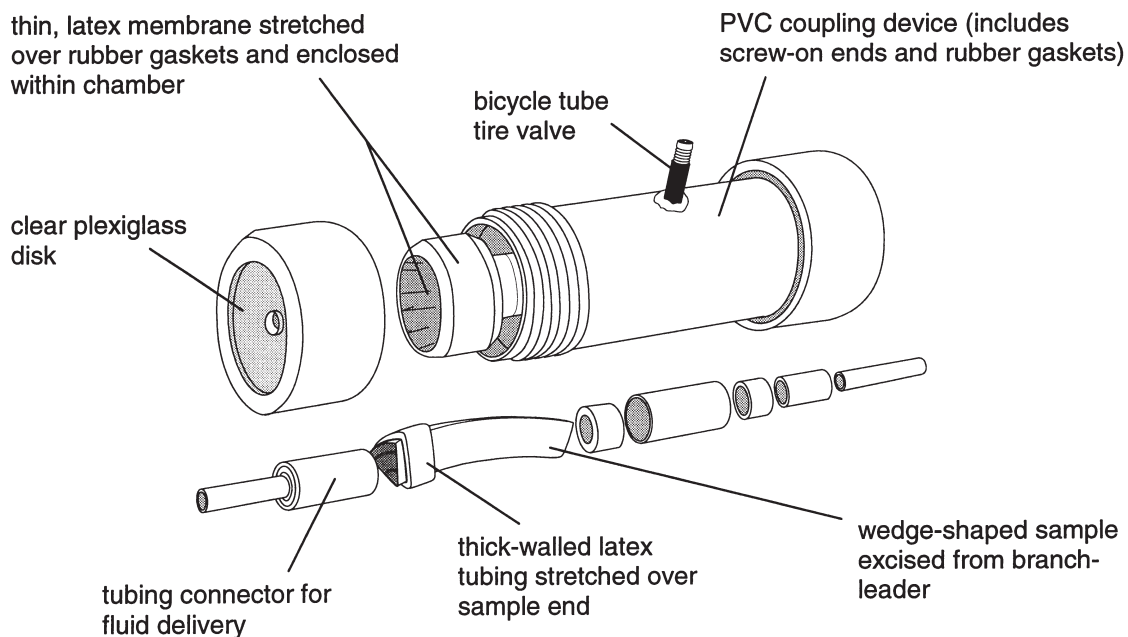


Figure 2. Pressure-sleeve apparatus and branch-leader subsample fitted with connectors. During conductivity measurements the subsample rests inside the latex membrane. Pressurizing the air inside the chamber forces the membrane against the sides of the sample and prevents leakage of the permeating fluid from the radial surfaces of the sample.

	$k_h (\times 10^{-8})$	$k_s (\times 10^{-4})$	$k_l (\times 10^{-7})$	Distal leaf area (cm ²)	$H (\times 10^{-4})$
Branch					
Age 1	1.0 ± 0.1 ^d	10.3 ± 0.7 ^b	5.7 ± 0.3 ^d	170 ± 10 ^d	5.8 ± 0.4 ^c
Age 3	6.0 ± 0.5 ^c	6.7 ± 0.5 ^{cd}	1.6 ± 0.1 ^f	3970 ± 320 ^c	2.4 ± 0.1 ^d
Branch-leader					
Age 1	4.2 ± 0.5 ^c	9.2 ± 0.6 ^{bc}	17.9 ± 1.3 ^b	230 ± 23 ^d	21.1 ± 2.2 ^b
Age 3	23.4 ± 2.8 ^b	6.7 ± 0.5 ^d	3.4 ± 0.3 ^e	6850 ± 590 ^b	5.1 ± 0.2 ^c
Leader					
Age 1	5.1 ± 0.5 ^c	8.4 ± 0.6 ^{bd}	26.9 ± 2.2 ^a	210 ± 20 ^d	33.5 ± 2.7 ^a
Age 3	101.9 ± 7.5 ^a	15.1 ± 0.6 ^a	8.0 ± 0.6 ^c	13150 ± 970 ^a	5.3 ± 0.3 ^c

Table 1. Hydraulic and foliar properties for each shoot type and segment age (mean ± standard error (SE), $n = 15$). Within each column, means with the same letter are not significantly different at the 0.05 level (univariate repeated measures procedure using a mixed model). Units for hydraulic parameters are as follows: k_h , m⁴ s⁻¹ MPa⁻¹; k_s and k_l , m² s⁻¹ MPa⁻¹

Branches and branch-leaders had higher k_s for 1-year-old than for 3-year-old segments, but the reverse was true for leaders. Distal leaf area was, of course, higher for all 3-year-old segments than for 1-year-old segments, but the magnitude of this difference varied significantly among shoot types, being greatest for leaders, intermediate for branch-leaders, and smallest for branches.

A comparison of same-aged segments among the three different shoot types revealed several interesting patterns. Among 1-year-old segments, k_h of leaders and branch-leaders was similar and, in both cases, significantly higher than that of branches. Among 3-year-old segments, k_h was highest for leaders, intermediate for branch-leaders, and lowest for branches. Specific conductivity (k_s) of 1-year-old segments did not differ among shoot types. Three-year-old branch and branch-leader segments did not differ significantly in k_s , but both had significantly lower k_s than 3-year-old leader segments. Huber value (H , ratio of sapwood area to leaf area) was highest for leaders, intermediate for branch-leaders, and lowest for branches among 1-year-old segments. In contrast, Huber values of 3-year-old leader and branch-leader segments were similar but significantly higher than those of 3-year-old branch segments. Leaf-specific conductivity (k_l) of 1- and 3-year-old segments followed a pattern identical to that of H with one exception: among 3-year-old segments, branch-leaders were significantly lower than leaders.

The relationship with sample diameter differed for k_s and k_l (Fig. 3). The diameter of branch-leaders was intermediate between branches and leaders for both 1- and 3-year-old segments. Within each shoot type, 3-year-old segments had consistently larger diameters and smaller k_l than 1-year-old segments. The same pattern held for k_s of branches and branch-leaders: k_s was lower for 3-year-old than for 1-year-old segments, despite their larger diameter. In contrast, 3-year-old leader segments had both larger diameters and higher k_s than 1-year-old segments.

Branch-leader subsamples: compression, opposite and lateral woods

Among subsamples taken from 3-year-old branch-leader segments, compression wood had significantly lower k_s than both opposite and lateral wood (Table 2).

Compression and opposite wood had, respectively, 21 ± 3 and 65 ± 7% [mean ± standard error (SE)] the k_s of lateral wood. In all but two cases, lateral wood had the highest k_s among the three types of wood. Compression wood samples had a larger mean radius than either lateral or opposite wood samples.

DISCUSSION

Fifteen months after leader removal, branch-leaders were intermediate between branches and leaders in their ability to supply foliage with water (as quantified by k_l for both 1- and 3-year-old segments). This implies that a steeper water potential gradient would develop in branch-leaders, relative to normal leaders, under the same transpiration rate (Zimmermann 1978). Subject to lower water potentials, branch-leaders would then be at greater risk of cavitation and more quickly limited in gas exchange by stomatal closure (Sperry 1986; Sperry & Pockman 1993; Sperry, Alder & Eastlack 1993). To examine the effect on whole shoot water relations, future work should include measurement of stomatal conductance and water potential gradients along shoot axes.

Despite this limitation imposed by xylem anatomy on the conductive efficiency of branch-leaders, after 15 months they were clearly in transition towards assuming the favoured hydraulic status of a leader. The observed increase in both H and k_l towards the top of the main stem, both for normal leaders and, to a lesser extent, branch-leaders, is consistent with a pattern of strong apical control (Ewers & Zimmermann 1984a; Sellin 1987). In leaders, this distal increase in conducting area per unit foliage more than compensates for declining values of k_s towards the top of the main stem, allowing for greater rates of elongation and facilitating height growth.

Among 1-year-old segments, differences in k_l were the result of differences in H rather than in k_s . Differences in k_l among 3-year-old segments were the result of more complex interactions. Three-year-old leaders and branch-leaders had very similar H but differed in k_s : in this case, the high k_l of the leader is the result of high k_s . In contrast, 3-year-old branch-leader and branch segments had nearly identical k_s but differed in H : the high k_l of the branch-leader is the result of a larger conducting area per unit

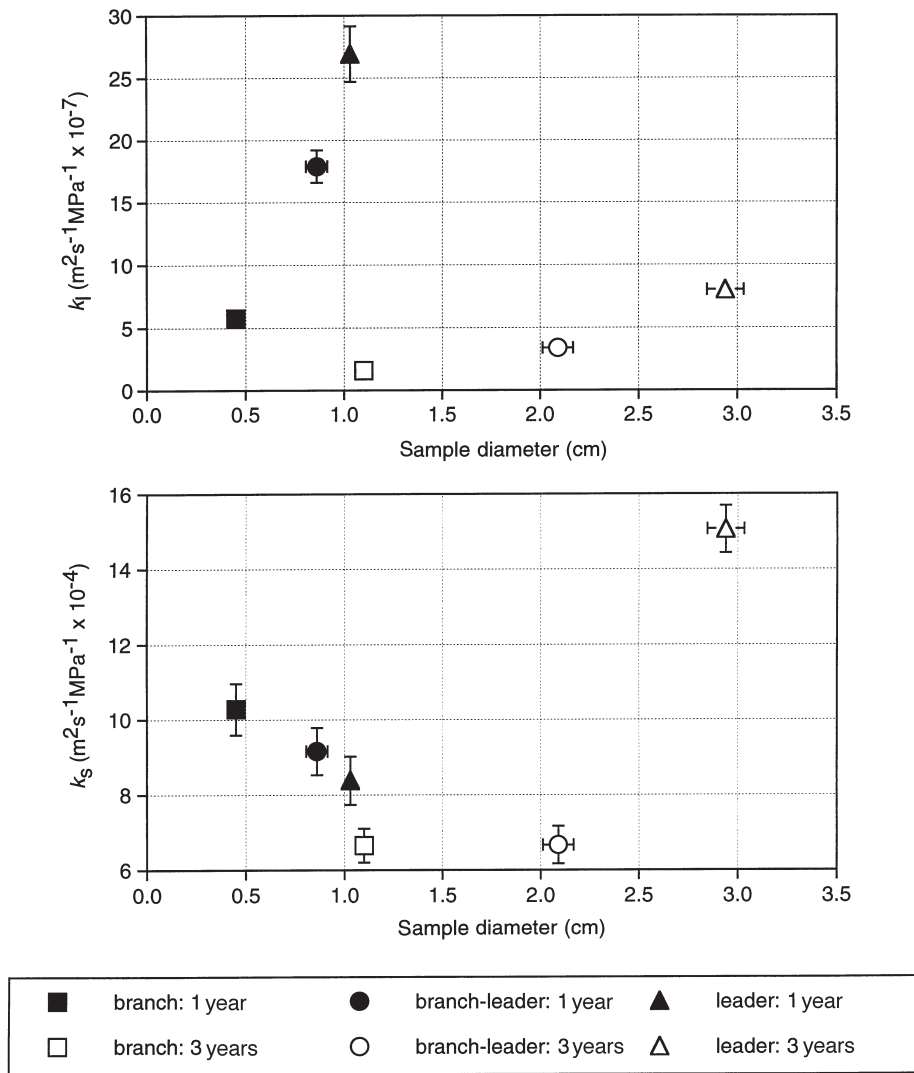


Figure 3. Mean k_1 and k_s as a function of mean sample diameter ($n = 15$). Symbols represent means, error bars show standard error for k_s , k_1 (vertical) and diameter (horizontal). Closed symbols represent 1-year-old segments; open symbols represent 3-year-old segments. Squares represent branches; circles represent branch-leaders; triangles represent leaders.

foliage. The high k_1 of 3-year-old leader segments in relation to branch segments can be attributed to both a high k_s and H .

Shoot types differed with respect to changes in k_s between 1- and 3-year-old segments. The k_s of leader segments increased with age, and therefore with sample diameter. In contrast, k_s of branches, and to a lesser extent,

branch-leaders, actually decreased with age, and therefore with sample diameter. Given the location of samples within each shoot, this is consistent with observations of peak k_s values occurring near the middle of shoot axes and declining towards both the tip and base (Ewers & Zimmermann 1984a,b; Sellin 1987, 1988, 1994). While 3-year-old segments came from the most basal region of

	Compression wood	Opposite wood	Lateral wood
k_s ($\text{m}^2 \text{s}^{-1} \text{MPa}^{-1} \times 10^{-4}$)	2.2 ± 0.3^a	6.9 ± 0.8^b	11.5 ± 1.3^c
Mean sample radius (mm)	11.0 ± 0.5^a	8.3 ± 0.4^b	8.9 ± 0.4^c

Table 2. Specific conductivity (k_s , $\text{m}^2 \text{s}^{-1} \text{MPa}^{-1} \times 10^{-4}$) and dimensions of subsamples from regions of compression, opposite and lateral wood within 3-year-old branch-leader segments (mean \pm standard error (SE), $n = 15$). Within each row, means with the same letter are not significantly different at the 0.01 level (differences between any two wood types based on paired t -tests)

branches and branch-leaders, they came from a region near the top of the main axis in the case of leader segments. This axial change in k_s results from developmental changes in tracheid dimensions (Duff & Nolan 1953; Dinwoodie 1961; Larson 1969; Megraw 1985; Aloni 1987). While the decrease in tracheid size towards the tip of a trunk or branch is the result of a decrease in cambial age, the cause of the decrease observed towards the base may relate to xylem mechanical requirements, and may differ between shoot types (Panshin & de Zeeuw 1980; Zobel & van Buijtenen 1989). It is not known to what extent compression wood is responsible for the decline in k_s towards the base of branches.

The k_s of branches was lower than that of leaders among 3-year-old segments, but the two shoot types did not differ in k_s among 1-year-old segments. This pattern has also been observed in *Abies balsamea* (Ewers & Zimmermann 1984a). As a general rule, branches have lower k_s than leaders, but this pattern is a function of the rate at which tracheid dimensions increase with cambial age rather than an inherent difference in size. Differences in tracheid dimension between branch and stem wood are not likely to be significant in the first ring from the pith but increase rapidly moving towards the bark (Park, Saiki & Harada 1979), with older stems having much larger tracheids than branches of the same age. In addition, compression wood is often sparse or lacking in the first ring from the pith in branch wood (Little 1967; Park *et al.* 1979).

It is not possible to tell from the current study whether the lower k_1 of 3-year-old segments from branch-leaders versus leaders is due to the presence of a 2-year-old core of branch wood, the presence of large amounts of compression wood, or a combination of both. In order for compression wood to produce no net effect on the whole shoot level (i.e. if its low permeability did not reduce overall permeability), some other aspect of xylem anatomy would have to act in 'hydraulic compensation'. Among segments excised from basal (3-year-old) samples of branch-leaders, both compression and opposite wood had lower k_s than lateral wood. This suggests that opposite wood does not compensate for the reduced k_s of compression wood, but rather adds to it. This result is also consistent with observations that opposite wood tracheids are intermediate in size between those of compression and lateral wood (Nicholls 1982; Park 1983, 1984a,b, 1986), and that opposite wood has a higher proportion of latewood than compression wood (Wood & Goring 1971). Although radial growth in the compression wood region is high relative to regions of opposite and lateral wood, it is unlikely that this could make up for the low k_s of compression wood. The cross-sectional area of compression wood would have to be more than five times that of lateral wood in order for the two wood types to produce equal flow rates, and this is clearly not the case.

Fifteen months after leader removal, 3-year-old branch-leader segments had low permeability and a high ratio of sapwood area to leaf area relative to branches. These structural changes are consistent with an increase in xylem

mechanical requirements (Gartner 1991; Dean 1991). Indeed, the 3-year-old portion of branch-leaders contained nearly all of the compression wood responsible for reorientation of the shoot. In spite of this mechanical requirement, basal branch-leader segments could supply foliage with water more efficiently than branches. It seems likely that with one or more years of xylem production, the basal region of branch-leaders will have the same k_1 as intact leaders. In contrast, it is surprising that 1-year-old branch-leader segments, which had no special mechanical requirements, had lower k_1 (attributable entirely to lower H) than those of leaders. It may be that new branch-leader growth (produced entirely in the absence of a leader) is limited by the xylem transport efficiency of more basal regions. It is also important to note that these structural changes may occur solely in response to new mechanical requirements, with incidental changes in hydraulic properties. Further research is needed to improve our understanding of how the mechanically specialized compression wood influences shoot water relations.

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