AN ABSTRACT OF THE THESIS OF

Rachel Spicer for the degree of Master of Science in Forest Products and Forest Science presented on July 2, 1997. Title: Hydraulic Properties of Compression Wood in Branches and Reoriented Shoots of Douglas-fir (Pseudotsuga menziesii)

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Xylem anatomy is a strong determinant of water transport efficiency and is therefore an important component of the overall hydraulic strategy of any woody plant. However, in addition to its role in water transport, xylem also serves in mechanical support, and these two functions may represent conflicting design requirements. To further our understanding of how mechanical requirements might affect water transport in woody plants, this research evaluates the efficiency with which compression wood, which is specialized to function in mechanical support, conducts water. Using young Douglas-fir (Pseudotsuga menziesii) trees, two modes of compression wood formation are considered: normally-growing branches and branches that take over as leaders.

Lower branch halves, which contained large amounts of compression wood, were significantly limited in their ability to conduct water relative to upper halves. This is likely a result of their anatomy, as lower halves were denser and had shorter tracheids with narrower cell lumens than upper halves. Compression wood samples from branches that had taken over as leaders were also limited in their ability to conduct water, relative to samples from the wood formed opposite and to the sides of compression wood. In

addition, compression wood samples from branches that had taken over as leaders were less permeable than lower branch halves.

Despite the poor transport efficiency of lower branch halves, the amount of compression wood visible on the end of each branch segment did not explain any significant variation in whole segment hydraulic properties. This lack of relationship between compression wood and whole segment properties suggests that branches may make up for the lost conductive capacity in some way. In branches that replaced a missing leader, there was no evidence that xylem formed elsewhere in the segment (i.e., "opposite wood") made up for the loss through a concomitant increase in permeability. Instead, branches that replaced leaders increased their transport efficiency relative to normal branches through an increase in conducting cross-sectional area. Given the reduced permeability of compression wood, future work should address how woody plants minimize or counteract the detrimental effects of this mechanically-specialized xylem to fulfill their water transport needs.

Hydraulic Properties of Compression Wood in Branches and Reoriented Shoots of
Douglas-fir (*Pseudotsuga menziesii*)

by

Rachel Spicer

A Thesis Submitted
to
Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented on July 2, 1997
Commencement June 1998

ACKNOWLEDGEMENTS

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Chapter 1

Introduction

HYDRAULIC ARCHITECTURE OF GYMNOSPERMS

General concepts in hydraulic architecture

An adequate supply of water to the leaves of a woody plant is critical to maintain gas

exchange and the production of photosynthates. One potential limit on the flow of water

to leaves is the resistance imposed by the xylem itself. The xylem structure of woody

plants is far from uniform. Patterns of variation in the permeability and quantity of

xylem, relative to the amount of foliage supplied by the xylem, have both physiological

and ecological consequences. The hydraulic architecture of any woody plant is therefore

an important component of an overall hydraulic strategy.

Leaf-specific conductivity (LSC, also k_l) describes the ability of a given segment

of xylem to supply water to the foliage distal to that segment, and is defined as

$$LSC = \frac{Ql\eta}{A\Delta P},$$

where LSC is in m^2, Q is the volume flow rate (m^{3}s^{-1}), l is the length of the segment (m), η is the dynamic viscosity of the sap or permeating fluid (1.008 x 10^{-3} Pa s (= N s m^{-2}) at 20°C, Jones 1992), A is the area of foliage distal to the segment (m^2, sometimes replaced by the fresh weight of foliage), and ΔP is the pressure difference between the two ends of the segment (Pa) (Zimmermann 1978).

At a given transpiration rate, LSC (ignoring water storage capacitance, and removing the term for dynamic viscosity included in the above definition of LSC) determines the pressure gradient (dP/dx) through a stem segment following the relationship

$$\frac{\mathrm{d}P}{\mathrm{d}x} = \frac{E}{LSC},$$

where E is the mean evaporative flux density (m^{3}s^{-1}m^{-2}) of the foliage supplied by the stem segment (Zimmermann 1978, Tyree and Ewers 1991). This equation shows the physiological relevance of LSC by demonstrating that the lower the LSC, the steeper the pressure gradient required to supply foliage with water for a given transpiration rate. Increased xylem resistance can then limit gas exchange and the production of photosynthates by affecting stomatal behavior. Reduced hydraulic conductance (reciprocal of resistance) has been shown to cause stomatal closure (Borghetti et al. 1989, Sperry 1986, Sperry and Pockman 1993, Sperry et al. 1993) and is a likely cause of reduced stomatal conductance in long, relative to short, branches of *Pinus radiata* (Waring and Sylvester 1994). Recent evidence suggests that reduced hydraulic

conductance in old trees of *Pinus contorta* and *Pinus ponderosa* causes early daily stomatal closure relative to young trees, and may account for reductions in net photosynthesis observed with age (Yoder et al. 1994). Similarly, age-related changes in whole-tree, aboveground LSC in *Pinus sylvestris* parallel changes in "growth efficiency" (E_g, biomass increment per unit leaf area, defined in Waring 1983) (Mencuccini and Grace 1996b). Scaling-up from the tree to the stand, age-related changes in aboveground stand hydraulic conductance parallel changes in net primary productivity (Mencuccini and Grace 1996b).

The LSC of a segment is determined not only by the amount of foliage supplied by the stem, but also by the quantity and permeability (k_s, defined below) of the xylem. The Huber value (HV) is a unitless ratio describing the relative quantities of xylem and foliage, and is defined as the ratio of sapwood (or whole stem) cross-sectional area (m^2) to the leaf area (m^2) distal to a stem segment (Huber 1928). It follows that

$$LSC = HV \times k_s.$$

Within- and between-plant differences in LSC can then be broken down into components. Supported stems (e.g., by staking or guying) typically have lower HVs than unsupported stems, allowing for higher k_s in the absence of xylem mechanical requirements (Gartner 1991a, b; Dean 1991). As a result HV is often considered largely of mechanical value. It should be noted, however, that increasing the amount of xylem per unit leaf area (i.e., increasing HV) can also be an effective means of increasing LSC (e.g., in response to water stress; Shumway et al. 1991, 1993).

Observed patterns of hydraulic architecture in gymnosperms

The most commonly observed pattern in hydraulic architecture is a hierarchy of LSCs with branching order. Trunks consistently have higher LSCs than lateral branches, first-order branches have higher LSCs than second-order branches, and so forth. Among gymnosperms, this pattern has been noted in *Tsuga canadensis* (Ewers and Zimmermann 1984b), *Abies balsamea* (Ewers and Zimmermann 1984a), *Picea abies* (Sellin 1988) and *Thuja occidentalis* (Tyree et al. 1983). Hydraulic constrictions (regions of low LSC) have been found in the branch junctions of *T. canadensis* (Ewers and Zimmermann 1984b), *T. occidentalis* (Tyree et al. 1983) and *P. abies* (Sellin 1988), and non-functional, circular tracheids have been found in the junctions of *Cupressus sempervirens* and three *Pinus* species (Lev-Yadun and Aloni 1990). These two patterns taken together restrict the greatest tensions (=lowest pressures) to the most distal organs (e.g., twigs and leaves) and reduce the risk of cavitation in the main stem during severe drought. This form of hydraulic plant segmentation exists in both gymnosperms and angiosperms and is interpreted as a safety mechanism, allowing plant parts that represent the lowest investment to be sacrificed in times of water stress (Zimmermann 1978, 1983; Tyree and Alexander 1993).

In the absence of transpiration, the hydrostatic pressure of water alone creates a water potential gradient (0.098 MPa for every 10 meters in height) along the main axis of a tree. While leaves at the apex of a tree are arguably most important in terms of height growth and competition for light resources, a hydraulic disadvantage is inherent to their position. The maintenance of high LSC at the stem apex and, in some cases, an acropetal

increase in LSC, at least partially compensates for this and has been observed in *P. abies* (Sellin 1987, 1994) and *A. balsamea* (Ewers and Zimmermann 1984a). Due largely to an increase in HV rather than any change in k_s, this pattern of LSC along the main axis is considered a hydraulic expression of apical control favoring elongation growth of the leader (Huber 1928, Ewers and Zimmermann 1984a). Individuals of *T. canadensis* (Ewers and Zimmermann 1984b), and stunted or suppressed individuals of *P. abies* (Sellin 1987, 1994) and *A. balsamea* (Ewers and Zimmermann 1984a), all of which exhibit weak apical control, show an acropetal decrease in LSC, often due to an acropetal decrease in HV.

Trends in hydraulic properties along branch axes have received less attention but there does appear to be a pattern in LSC and HV. Primary branches of *P. abies* sampled at fixed distances from the stem show LSCs that peak in the middle and decline slightly toward the branch base and tip, while HVs remain constant and increase sharply only at the branch tip (Sellin 1994). Unlike trends along the main stem (trunk), this pattern holds for both vigorous and stunted individuals. Primary branches of *A. balsamea* (Ewers and Zimmermann 1984a) and *T. canadensis* (excluding those branches that were once leaders) (Ewers and Zimmermann 1984b) show similar acropetal changes in LSC and HV. I have looked at primary branches in the top 6 whorls of mature *Pseudotsuga menziesii* and found a) a sharp increase in LSC at the branch tip due to an increase in HV, and b) a slight decrease in LSC toward the branch base due to decreases in both HV and k_s (unpublished data).

PERMEABILITY AND GYMNOSPERM XYLEM ANATOMY

Beyond the pipe model theory

The pipe model theory of plant form considers stems as a collection of pipes, each supplying a unit of foliage with water (Shinozaki et al. 1964). While the resulting functional relationship between sapwood area and leaf area has proved invaluable to ecologists (Grier and Waring 1974; Waring et al. 1977, 1982; Whitehead 1978), at the finer scales relevant to physiology we know the pipe model to not be strictly true (Huber 1928, Brix and Mitchell 1983, Whitehead et al. 1984, Gartner 1991a). Patterns of variation in xylem anatomy within a single plant stem create localized differences in xylem permeability, which in turn allow for a non-constant relationship between stem cross-sectional area and foliage.

Flow through plant stems at a number of scales can be thought of as analogous to Ohm's law, where anatomical structures represent resistance to flow and are summed in parallel and in series (see Richter 1973 for a discussion of this approach and its limitations). Water flow in gymnosperm xylem occurs through non-living tracheids connected by pairs of bordered pits, which in turn contain a porous membrane (the margo). At the finest scale, flow is governed by the dimensions of margo pores, pit apertures and tracheid lumens (Bolton and Petty 1978, Gibson et al. 1985). At a coarser scale, like that of the whole plant, flow is governed not only by the resistance of a catena of xylem components (e.g., root, stem, branch, petiole, leaf vein), but also soil resistance, actively-regulated stomata and boundary layers around the leaves (Tyree et al. 1975, Edwards et al. 1986, Tyree and Ewers 1991, Mencuccini and Grace 1996a, b).

Poiseuille's law and the importance of conduit size

Poiseuille's law describes laminar fluid flow through an ideal capillary (or bundle of capillaries, see Tyree and Ewers 1991) and states that flow rate is proportional to the fourth power of the capillary radius. This law is frequently used to model xylem transport because it illustrates the importance of small changes in conduit diameter, a measurement obtained with relative ease. Not surprisingly, measured permeability is usually much less (up to 80% less) than theoretical permeability based on Poiseuille's law (Gibson et al. 1985, Calkin et al. 1986, Pothier et al. 1989a). Reasons for this disagreement in gymnosperms are many. Rather than perfect capillaries, tracheids are typically rectangular in cross-section, often have textured or sculptured walls, and are connected by small diameter pits (2 to 20μm) with even smaller diameter membrane pores (0.1 to 2μm) (Panshin and de Zeeuw 1980, Siau 1995). Accounting for this pit membrane resistance improves the agreement between calculated and measured flow rates (Gibson et al. 1985, Calkin et al. 1986). The effect of pit resistance apparently increases as tracheid diameter increases and tracheid length decreases (Calkin et al. 1986, Pothier et al. 1989a). The importance of accounting for conduit shape has also been stressed (Lewis and Boose 1995). Corrections applied to Poiseuille's law to account for elliptical, rectangular and triangular conduit cross-sections actually *increase* the discrepancy between measured and theoretical flow rates, indicating an even greater need to identify the cause of these differences. Finally, evidence from gas permeability measurements suggests that at very high flow rates, bordered pit openings act as short capillaries causing nonlinear flow, a point at which both Poiseuille's law and Darcy's law

(defined below) become inapplicable (Kuroda and Siau 1988). This observation underscores the need to use realistic (i.e., those found in nature) flow rates for physiological permeability measurements.

Patterns of permeability as they relate to xylem anatomy

Measured flow rates are used to calculate permeability according to Darcy's law, defined here as

$$k_s = \frac{Ql\eta}{A\Delta P},$$

where k_s is permeability (generally referred to as specific conductivity or relative conductivity in plant physiology literature) in m^2, Q is the volume flow rate (m^3/s), l is the sample length (m), η is the dynamic viscosity of the sap or permeating fluid (1.008 x 10^{-3} Pa s (= N.s m^{-2}) at 20°C, Jones 1992), A is the cross-sectional area of conducting xylem (usually determined by dye perfusion), and ΔP is the pressure difference between the two ends of the segment. Application of Darcy's law to steady state flow through green wood produces flow rates that are linearly related to applied pressure gradients and are independent of the direction of flow (Comstock 1965, Puritch 1971, Edwards and Jarvis 1982).

Patterns of within-tree variation in k_s follow trends expected from developmental changes in xylem anatomy (see Gartner 1995 for review). A general hierarchy of k_s exists

within gymnosperms such that xylem components, ranked from high to low k_s, follow the order of root, trunk, first-order branch, second-order branch, third-order branch (Sellin 1988; Ewers and Zimmermann 1984a, b). Within a single axis (e.g., a trunk or first-order branch), k_s tends to peak in the middle and decline both in the direction of the tip and, to a lesser extent, the base (Sellin 1994, 1987, 1988; Ewers and Zimmerman 1984a, b). Consistent with this are observations of peak permeability near the base of the live crown in mature *Pinus radiata* (Booker and Kininmonth 1978), *Pinus contorta* and *Picea sitchensis* (Whitehead et al. 1984), *Pinus banksiana* (Pothier et al. 1989b), and *Pinus sylvestris* (Mencuccini and Grace 1995, 1997). Branches follow a similar trend with their height above ground: peak k_s values from the mid-sections of *Picea abies* branches at three heights were highest for the intermediate height and decreased both toward the top and base of the tree (Sellin 1993). Variation in k_s within an organ is more difficult to measure. Nevertheless, radial increases in k_s from pith to bark (excluding heartwood, which is non-conductive) have been shown for stems of *Abies grandis* (Puritch 1971) and roots of *Picea abies* and (Sellin 1990a).

Not surprisingly, trees grown under favorable environmental conditions tend to have high overall k_s relative to those grown in poor conditions. For *Picea abies*, poor light (shade) and poor soil (bog-grown) conditions both produced trees with lower k_s values than trees grown in full light or well-drained soil (Sellin 1994, 1993). Similarly, the k_s values of *Pinus banksiana* show a positive relationship with site index (Pothier et al. 1989b).

Variation in measured sapwood permeability has been experimentally related to a number of xylem characteristics. Of particular importance in large tree stems is relative

water content (percent of void space actually occupied by water), which, in essence, governs the amount of xylem truly functioning in water transport. Sapwood permeability decreases with decreasing relative water content, making the distinction between saturated and non-saturated permeability an important one, particularly late in the temperate-zone growing season when a significant proportion of the xylem may be embolized (air-filled) (Puritch 1971; Edwards and Jarvis 1982; Pothier et al. 1989a; Sellin 1990b, 1991). As a result, relative water content is used as a major determinant of k_s to model diurnal and seasonal flow through the whole trees (Edwards et al. 1986). Saturated sapwood permeability correlates well with tracheid lumen diameter and length (Ewers and Zimmermann 1984b; Pothier et al. 1989a, Sellin 1990b, Coyea and Margolis 1992), and not surprisingly, tracheid lumen radius raised to the fourth power (Ewers and Zimmermann 1984a).

COMPRESSION WOOD FORM AND FUNCTION

Occurrence, function and action of compression wood

Compression wood is a type of reaction wood that forms on the undersides of branches and leaning stems as a means of mechanical support in trees belonging to Coniferales, Ginkgoales and Taxales (Timell 1983). Most evidence suggests that the stimulus for compression wood formation is a change in orientation within a gravitational field, rather than a stress/strain stimulus produced by bending (Sinnott 1952, Westing 1968, Wilson and Archer 1977). Vertically growing (orthotropic) stems and plagiotropic branches have a predetermined equilibrium position (EP), such that movement out of this position

stimulates compression wood formation that will return the shoot to its EP (Little 1967, Wilson and Archer 1974). Even in the absence of external forces (e.g., caused by wind or snow), branches are moved out of their EP annually by increasing self-weight as a result of their plagiotropic habit (Wilson and Archer 1974, 1981). Branch compression wood then differs from stem compression wood in that it is a normal, rather than abnormal, occurrence.

Reorientation of the shoot is brought about by the generation of internal bending moments resulting from growth strains and stresses in differentiating compression wood tracheids (Boyd 1973, Wilson and Archer 1977, Wilson 1981, Yamamoto et al. 1991). Changes in tracheid dimensions produce growth strains (changes in unit length per unit length) during cell differentiation (Archer and Wilson 1973, Archer 1987). These strains then translate into stresses (forces per unit area) because differentiating cells are cemented to adjacent mature cells. Whereas normal wood cells generate tensile strains and stresses (i.e., they tend to contract), compression wood cells tend to elongate during differentiation and generate large compressive strains (Wilson and Archer 1977). The resulting compressive stress produces the internal bending moment responsible for reorientation of the shoot. There are a number of hypotheses regarding the origin of the initial growth strain (i.e., the cause of the dimensional change; see Wilson 1981, Wilkins 1986 for reviews). Most evidence suggests that the unusually high microfibril angle in the S_2 layer of compression wood tracheids (see below) results in elongation during lignification, as the deposition of lignin causes swelling between the cellulose microfibrils (Boyd 1972, 1973; Yamamoto and Ojuyama 1988; Yamamoto et al. 1991).

Anatomy of compression wood

The anatomy of compression wood was first described by Karl Sanio in 1860 (Timell 1980) and has since been the focus of an enormous body of work (for reviews see Westing 1965, 1968; Timell 1986). Compression wood is extremely dense (1.1 to 1.3 times the density of normal wood, Panshin and de Zeeuw 1980) and forms annual rings wider than those of normal wood, resulting in eccentric growth about the pith. Compression wood tracheids are round in outline, leaving intercellular spaces, and tend to be short and thick-walled due to both an accelerated rate of cell division and an extended duration of secondary wall deposition (Kennedy and Farrar 1965, Yoshizawa et al. 1985a, Nix and Brown 1987). Tracheids with deformed or bifurcated tips are often observed in compression wood, and their frequency is positively correlated with both a high frequency of cell division and the angle of lean in stems (Yoshizawa et al. 1985b, 1987). In some instances, traumatic vertical resin canals have been associated with compression wood formation (Lee and Eom 1988, Core et al. 1961).

Cell wall ultrastructure of compression wood also differs from that of normal wood. Compression wood tracheids lack the normal S_3 layer and in its place have a thick, highly-lignified S_2 layer with a high microfibril angle, sometimes referred to as a separate $S_2(L)$ layer (Côté and Day 1965, Wood and Goring 1971, Boyd and Foster 1974, Siripatanadilok and Leney 1985, Timell 1986). In many species helical cavities (also referred to as radial checks) form in the cell walls of compression wood tracheids parallel to the angle of microfibrils and may represent a form of evolutionary specialization (Westing 1965, Timell 1983, Yoshizawa and Idei 1987). The abnormal ultrastructure of

compression wood tracheids affects the shape of bordered pits, which tend to be sunken deep in the cell wall, often located at the bottom of helical cavities. Tracheids in well-developed compression wood have fewer bordered pits on their radial walls and smaller pit apertures than those of normal wood (Lee and Eom 1988; Ohtani and Ishida 1981, as reviewed in Timell 1986).

The first-formed earlywood tracheids in an annual ring containing compression wood are often normal in appearance, and their quantity and anatomy depends on the severity of compression wood formation or degree of stem lean (Harris 1976, Yoshizawa and Idei 1987). These first-formed tracheids are thin-walled, squarish and lack helical cavities, but they have many characteristics typical of compression wood, including a high microfibril angle, absence of the S_3 layer, highly lignified S_2 layer, and short length, and can therefore not be considered normal (Côté et al. 1967, Höster 1974, Siripatanadilok and Leney 1985). In contrast to our knowledge of stems, we know little about the anatomy of first-formed earlywood tracheids in branches. Compression wood is sparse or lacking in the first annual ring (next to the pith) of some branches (Park et al. 1979). It may be that branches produce truly normal wood at the start of the growing season, before self-weight moves them out of their EP. In *Pinus strobus*, branches did not appear to produce compression wood until 20 days after the start of cambial activity (Wilson and Archer 1981), but the ultrastructure of the first-formed tracheids was not studied. At least one study suggests that earlywood tracheids in the annual rings of branches are normal in both appearance and anatomy (Schultze-Dewitz et al. 1971).

Anatomy of opposite wood

Compression wood is usually considered a distinct entity because it forms within annual rings as visually distinct, dark reddish-brown arcs. It is more accurate to consider a gradient of anatomical and growth stress characteristics about the circumference of a stem or branch containing compression wood. The wood formed to the sides of compression wood (termed "lateral wood") most closely resembles normal wood, while that formed directly opposite compression wood ("opposite wood") has, appropriately, characteristics opposite those of compression wood.

Opposite wood typically forms in very narrow annual rings with highly variable proportions of latewood (Timell 1973b, Lee and Eom 1988, Park 1986). Tracheids of opposite wood are thin-walled and square or rectangular in outline, possess all three normal cell wall layers (S_1, S_2, S_3) and have microfibril angles lower than those of normal wood (Timell 1973b; Boyd and Foster 1974; Park 1983, 1984a, 1986). In contrast, opposite wood appears to be identical to normal wood in terms of chemical content (e.g., lignin content) (Timell 1973a, Boyd and Foster 1974). Tracheid length in opposite wood is variable: there are reports of both longer (Nicholls 1982, Lee and Eom 1988) and shorter (Park 1984b) tracheids relative to those of compression wood.

Hydraulic implications of compression wood

The effect of compression wood on the water relations of gymnosperms has received surprisingly little attention. Well-developed compression wood clearly should be less permeable than normal wood, but the ability of a stem or branch to supply foliage with

water is determined by the anatomy of the entire shoot. While compression wood is expected to increase resistance to flow, first-formed earlywood tracheids, opposite wood and eccentric growth may all act in compensation to produce no net effect for the cross-section as a whole.

Dye ascent experiments in *Abies* spp. demonstrate that a special type of compression wood formed as a result of *Adelges piceae* (Balsam woolly adelgid) infestations is relatively impermeable (Mitchell 1967). While these experiments are frequently cited as evidence of reduced flow through living stems containing compression wood, infestations also cause other changes, including premature heartwood formation, which would clearly affect permeability (Puritch and Johnson 1971, Timell 1986). Indeed, more recent work has shown that infestations of the Balsam woolly adelgid reduce permeability even in the absence of compression wood formation (Puritch 1971, Puritch and Petty 1971).

There is also a surprising lack of literature on compression wood permeability from the utilization standpoint. Compression wood has a lower green moisture content (MC, mass of water in fresh wood expressed as a percent of dry weight) (Pillow and Luxford 1937), and reaches a lower fiber saturation point (FSP, moisture content at which cell walls are just saturated with water) than normal wood (Algren et al. 1972). Compression wood has also been shown to absorb and lose water at a slower rate than normal wood (Timell 1986), but no work has specifically measured axial (longitudinal) permeability of compression wood relative to normal wood. In addition, utilization-oriented work on wood-water relations is of limited use in physiological studies because most of it deals with wood below (or wood that was at one time below) FSP. Irreversible

changes in wood structure (namely, bordered pit aspiration) occur during drying and as a result, fluid flow through dried wood bears little resemblance to flow through a living tree.

CONCLUSION

Xylem mediates the transport of water through stems from the soil to the atmosphere. As a result, xylem structure plays an enormous role in determining the ecological success and productivity of an individual by affecting leaf-level processes that rely on the supply of water. Xylem structure varies among and within species, within individuals, and within organs. Patterns of xylem variation among organs affect the flow of water through trees such that the main stem is favored over the more expendable leaves and shoots. The hydraulic implications of *within-organ* xylem variation, particularly in gymnosperms, are not as well-known. In the case of sapwood, structural requirements for mechanical support and water transport may conflict. It is not known to what extent compression wood, which is specialized for mechanical support, affects water flow through organs or whole-plant water relations.

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Chapter 2

Hydraulic properties of Douglas-fir (*Pseudotsuga menziesii*) branches and branch halves with reference to compression wood

Rachel Spicer and Barbara Gartner

ABSTRACT

Douglas-fir (*Pseudotsuga menziesii*) branch segments were used to test the hypothesis that compression wood reduces xylem transport efficiency. Whole 3-year-old segments were first measured for specific conductivity (k_s, m^2), then split lengthwise into upper and lower halves, the latter containing all or most of the compression wood in the segment. Halves were then re-measured for k_s using a technique to prevent leakage of the permeating fluid during measurements. Lower branch halves had significantly lower k_s than upper halves (6.4 ± 0.3 vs. 9.3 ± 0.3, respectively [n = 36]), and despite their larger size, significantly lower hydraulic conductivity (k_h, m^4) than upper halves. Lower branch halves had higher specific gravity (0.51 ± 0.01 vs. 0.45 ± 0.01 [n = 36]), lower moisture content (123 ± 2% vs. 155 ± 3% [n = 36]), and larger proportions of volume occupied by both cell wall and air than did upper halves. Lower halves had more tracheids per annual ring than upper halves (73 ± 3 vs. 63 ± 2 per radial transect, respectively [n = 36]), but tracheids were shorter and had narrower lumens than those of upper branch halves. Differences in hydraulic properties between upper and lower halves suggest that compression wood does reduce xylem transport efficiency. In contrast, the amount of

compression wood in each sample did not explain any variation in whole (prior to splitting) sample hydraulic properties.

INTRODUCTION

Xylem serves both mechanical and hydraulic functions throughout the plant stem. Unlike angiosperm xylem, in which a great variety of cell types and configurations allow for specialization, the more primitive xylem of gymnosperms consists almost entirely of tracheids (90 to 94% by volume, Panshin and de Zeeuw 1980). This single cell type must then perform both mechanical and hydraulic functions. While it is often suggested that xylem formation represents a tradeoff between mechanical support and an efficient supply of water to the foliage, experimental evidence for such a tradeoff is mixed. Artificially-supported stems require a smaller cross-sectional area of xylem per unit foliage, relative to self-supported stems, suggesting a hydraulic cost for mechanical support (Gartner 1991, Dean 1991). In contrast, age-related changes in xylem development for self-supported stems do not suggest such a tradeoff (Mencuccini et al. 1997).

Gymnosperm xylem is far from uniform despite the dominance of a single cell type, and patterns of variation in tracheid dimension result in patterns of variation in both mechanical and hydraulic properties within a single stem (Zobel and van Buijtenen 1989, Gartner 1995). One example of this variation is compression wood, which forms in gymnosperms on the undersides of branches and leaning stems as a means of mechanical support (Sinnott 1952; Westing 1965, 1968; Boyd 1973). Typical compression wood is

much denser than normal wood, owing to wide annual rings composed of tracheids with small lumens and thick, highly lignified cell walls which differ in ultrastructure from those of normal wood (Côté and Day 1965, Kennedy and Farrar 1965, Côté et al. 1967, Yoshizawa and Idei 1987). Compression wood tracheids are also shorter than normal wood tracheids and frequently have distorted and bifurcated tips (Siripatanadilok and Leney 1985, Yoshizawa et al. 1985b, Yoshizawa and Idei 1987). Although compression wood is often considered a discrete entity, it is more appropriate to consider the anatomical characteristics associated with compression wood to form a continuum about the circumference of a stem or branch. The wood formed directly opposite compression wood (appropriately termed "opposite wood") typically forms narrow annual rings composed of thin-walled tracheids that are square in outline (Timell 1973b; Park 1983, 1984a, b; Lee and Eom 1988). Trends in tracheid length and lumen diameter are less clear (Park 1983, 1984a, b), but most investigators agree that the wood formed to either side of compression wood ("lateral wood") resembles normal wood most closely and forms an anatomical intermediate between compression and opposite wood.

Although the mechanical role of compression wood is clear (Archer and Wilson 1970, 1973; Boyd 1973; Wilson and Archer 1977), its hydraulic consequences are not. The short, small-diameter tracheids of compression wood should increase resistance to the flow of water through living trees (Bolton and Petty 1978, Calkin et al. 1986), but the anatomy of the entire shoot will determine how well supplied the foliage is with water. The wide growth rings associated with compression wood (growth is often eccentric about the pith) may compensate for its low permeability by creating a larger conducting area relative to normal wood. Increased permeability of opposite and/or lateral wood

could also compensate at the level of the whole shoot. Finally, the formation of several or more bands of earlywood tracheids that are normal in appearance, at the start of an annual ring containing compression wood (Core et al. 1961, Wood and Goring 1971, Yoshizawa et al. 1985a, Yoshizawa and Idei 1987), may counteract the expected hydraulic impact of compression wood.

Given the pervasiveness of compression wood in the lower portion of gymnosperm branches, it is surprising that among numerous studies on hydraulic architecture, the potential impact of this dense wood on shoot hydraulic properties has not been addressed. In the current study, we examine the hydraulic role of compression wood in branches of young Douglas-fir trees. We first compare the hydraulic properties of upper and lower branch halves to test the hypothesis that lower branch halves do, in fact, conduct water less efficiently than upper branch halves. We then describe the anatomy of the branch halves to account for observed hydraulic differences. Finally, we investigate the potential for a tradeoff between hydraulic and mechanical xylem functions by relating whole branch hydraulic properties to the amount of compression wood present in each shoot.

MATERIALS AND METHODS

Plant material

Three branches were harvested from each of 12 Douglas-fir (*Pseudotsuga menziesii* var. menziesii (Mirb.) Franco) trees from mid-June to early July 1995. The trees ranged in age from 8 to 12 years and were naturally regenerated, growing in an open field adjacent

to Peavy Arboretum at the Oregon State University McDonald Research Forest (44°39'34" lat., 123°14'01" long., 136 m elev.). Samples for conductivity measurements (1 per branch) were taken from the three-year-old portion (i.e., the third "interwhorl" from the tip) of the main axis of five-, six- and seven-year-old branches. In this way, sample age, normally a strong determinant of hydraulic properties, was held constant while providing a range in the amount of compression wood in each sample. Samples of this age and from these positions were also large enough to allow separation of upper and lower halves, but small enough to fit in the 1.5 cm diameter opening of the pressure-sleeve apparatus (described below)

Prior to branch harvest, the region to be sampled was marked and measured for its angle with respect to the vertical by lining the flat side of a protractor against the bottom of the marked region and reading the angle from a weighted string. To minimize tension in the xylem and reduce the risk of introduced emboli, whole branches were harvested pre-dawn and the cut ends were immediately immersed in water for transport to the laboratory. All conductivity measurements were made the day of branch harvest.

Whole branch segments

Sample preparation. While immersed in water, a segment about 5 cm long was excised from the main axis of each branch near the base of the three-year-old portion of the shoot. The bark was removed and the ends were shaved with a razor blade. The area of compression wood visible on the proximal end of each segment was traced onto acetate paper and later measured using the image analysis system described below for leaf area.

Segment diameter, length and pith diameter and were measured with calipers. The segments remained submerged in water at room temperature until conductivity measurements were made.

Leaf area. Foliage attached and distal to each branch segment was collected and separated into two age classes: current-year and non-current year. For each branch and age class, fresh needles were removed from 5 randomly-selected, 4 cm long sprigs and frozen until after conductivity measurements were made. The remaining foliage was dried in an oven for 48 hours at 60°C and weighed. The projected area (one side) of fresh foliage samples was determined using a video camera and NIH Image v. 1.52 on a Quadra 800 Macintosh. Area to weight ratios did not vary significantly with branch age and samples were pooled to yield the following conversions. The ratio of fresh area to dry weight was 85.5 ± 1.4 cm^2/g for current-year foliage, and 70.5 ± 0.6 cm^2/g for older foliage.

Specific conductivity. Specific conductivity (k_s) describes the permeability of a xylem segment and is defined by Darcy's law as

$$k_s = \frac{Ql\eta}{A\Delta P},$$

where k_S is in m^2, Q is the volume flow rate (m^3/s), l is the length of the segment (m), η is the dynamic viscosity of the permeating fluid (1.008 x 10^{-3} Pa s (= N s m^{-2}) at 20°C, Jones

1992), A is the sapwood cross-sectional area (m^2), and ΔP is the pressure difference between the two ends of the segment.

Whole branch segments were fit with flexible tubing and a dilute solution of oxalic acid (10 mol/m^3, filtered to 0.22μm) was delivered to the distal end under a gravitational pressure head of approximately 0.01MPa. Oxalic acid has been shown to prevent the decline in conductivity with time that is commonly observed during long measurement periods using distilled water (Zimmermann 1978, Sperry et al. 1988). The fluid was collected from the proximal end in small vials for periods of 1 min and weighed on an electronic balance. Volume flow rate was calculated as the mean of at least 5 collection periods. To determine dynamic viscosity, thermocouples were used to record the temperature of both the oxalic acid and the water in which samples were held prior to conductivity measurements.

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

$$k_h = \frac{Ql\eta}{\Delta P},$$

where k_h is in m^4 and all terms are defined as above for k_S. Not surprisingly, k_h shows a positive relationship with the diameter of the sample.

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

$$LSC = \frac{Ql\eta}{A\Delta P},$$

where LSC is in m^2, and all terms are defined as above for k_s, except A, which is defined as the sum of the leaf area (one side) both attached and distal to the segment. Huber value (HV) is defined as the ratio of xylem cross-sectional area to distal leaf area, and is therefore unitless. Note that

$$LSC = HV \times k_s.$$

Branch halves

Sample preparation. Following conductivity measurements on whole branch segments, each segment was split lengthwise through the pith (starting at the proximal end) while immersed in water using a razor blade and small chisel. In this way each segment was divided into upper and lower branch halves, the latter containing all or most of the compression wood in the segment (Figure 2.1). Halves were quickly surface dried with a towel and weighed for later water content determinations. Volume flow rates were then measured to calculate both hydraulic conductivity (k_h) and specific conductivity (k_s).

Preliminary tests showed that volume flow rates could be measured twice on the same sample, with several hours between measurements, without significantly affecting the results.
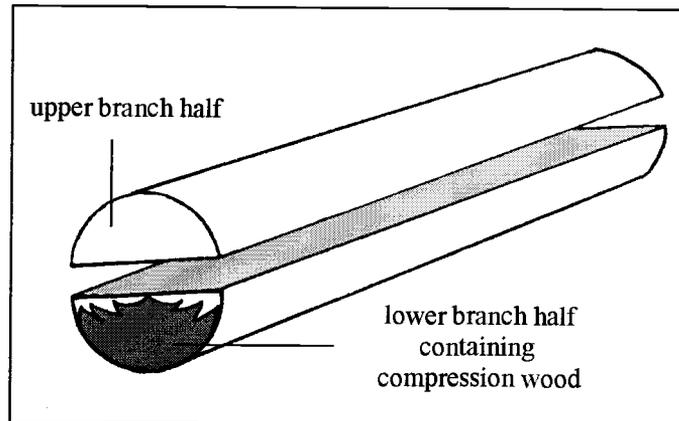
Figure 2.1. Branch segment split longitudinally into upper and lower halves.

Halves were not always equal in size, due both to the eccentric growth associated with compression wood and nature of splitting wood. The former determined the size of halves at the proximal end, where the samples were split directly through the pith, while the latter affected the size of halves at the distal end. For 15 samples (30 halves) an appreciable difference in size was noted and the cross-sectional area of both ends was measured on thin sections using the image analysis system described for leaf area. Cross-sectional area was then calculated as the mean of the area of the proximal and distal ends. For the remainder of the samples (42 halves), cross-sectional area was calculated only for the proximal end.

Pressure-sleeve apparatus. Branch halves were enclosed in a pressure-sleeve apparatus to seal the sides of the segments and prevent leakage during conductivity measurements. A double-ended pressure bomb (Sperry and Saliendra 1994) was modified to house a thin latex sleeve, which, upon pressurization of the air inside the chamber, was forced against the sides of the sample (see Figure 2.2). Latex sleeves of various sizes were made from cylindrical balloons by removing the closed end with a razor blade. Perfusion of branch halves with safranin-O and tests with impermeable plastic slugs in the shape of branch halves showed that an applied pressure of 0.1 MPa was sufficient to seal the sample sides under the range of gravitational pressure heads used here.
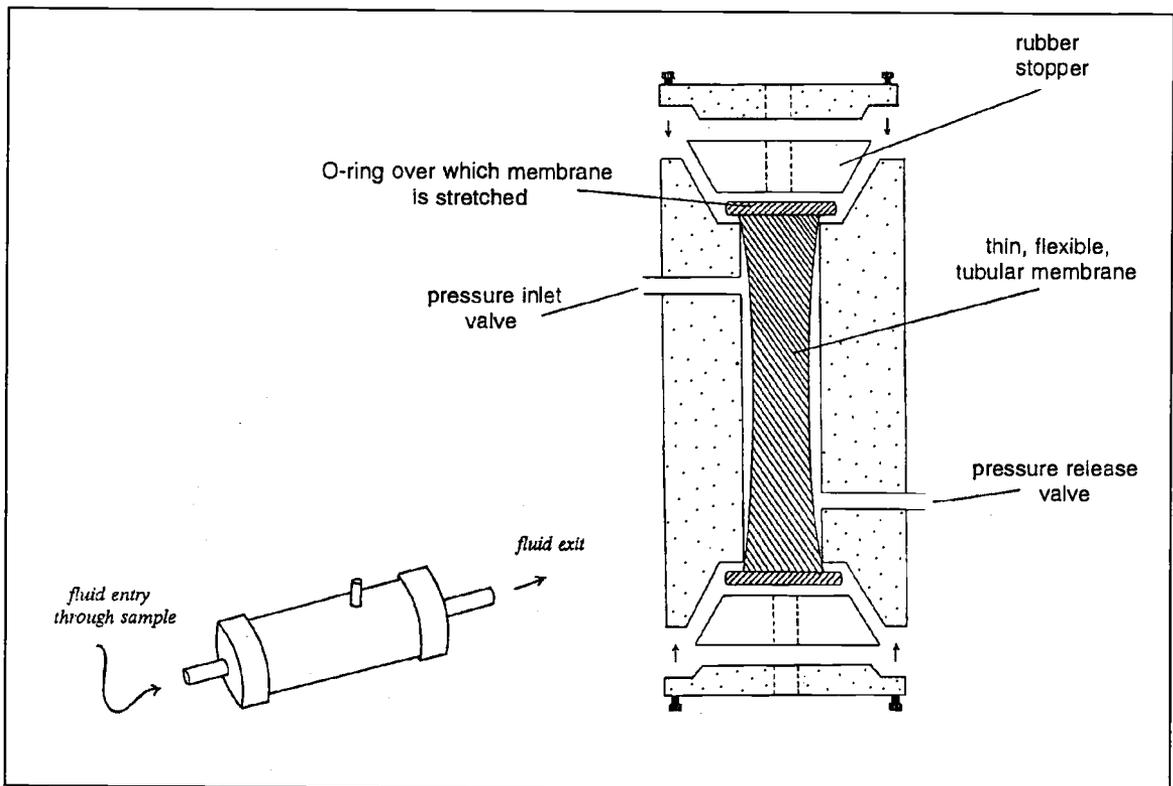
Figure 2.2. Pressure-sleeve apparatus.

Branch halves were fit at both ends with tubing connectors and inserted into the pressure-sleeve apparatus. Connectors consisted of thick-walled latex tubing that fit tightly around the end of each sample and attached to a 5-cm-long section of rigid plastic tubing via layers of smaller diameter, flexible tubing. Following a slow pressurization of the chamber, the connectors at either end of the segment were flushed with filtered oxalic acid (see above) to remove air bubbles, then attached to the reservoir of oxalic acid (distal end), and to a 1 ml graduated pipette (proximal end). Volume flow rates were measured under the same conditions described for whole branch segments by timing the movement of the meniscus across 0.01 ml intervals on the pipette. The mean of at least 8 timed intervals was used.

Following conductivity measurements, branch halves were perfused with filtered (0.22μm), 0.5% (w/v) safranin-O for 20 minutes. The earlywood always stained completely giving no evidence of cavitation. Branch halves were then measured for volume by water displacement, dried in an oven at 102°C for 48 hours, and weighed.

Damage estimates. Hydraulic conductivity (k_h) values were used to estimate the extent to which branch halves were damaged by the spitting process. For each sample, a "damage factor" (DF) was calculated as

$$DF = \left(1 - \frac{\text{UBH}k_h + \text{LBH}k_h}{\text{whole sample } k_h}\right) \times 100,$$

where UBH and LBH refer to upper and lower branch half, respectively.

Specific gravity. Specific gravity (SG) is a unitless ratio of oven-dry weight to the weight of water displaced by a sample at a given moisture content and was calculated as

$$SG = \frac{W_d}{V_f \times D_w},$$

where W_d is the dry weight of the segment (g), V_f is the fresh volume (cm^3) and D_w is the density of water (g/cm^3) (Siau 1984). Specific gravity should be constant at the moisture contents of fresh branch halves, which are above fiber saturation point (FSP, generally between 25 and 30%, below which shrinkage occurs, Panshin and de Zeeuw 1980).

Moisture content. Moisture content expresses the amount of water in wood per unit dry weight and was expressed as a percent

$$MC = \frac{W_f - W_d}{W_d} \times 100,$$

where all terms are defined as above for SG and W_f is the fresh weight of the segment (g).

Volume occupied by cell wall material, water and air. For each branch half, the volume occupied by cell wall material (e.g., cellulose, hemicellulose and lignin), water and air was expressed as a percentage of sample fresh volume. The percentage of volume occupied by cell wall material ($V_{cell\ wall}$) was calculated as

$$V_{cell\,wall} = \frac{W_d}{V_f \times 1.53} \times 100,$$

where terms are defined as above for SG and pure cell wall material is assumed to have a constant density of 1.53 g/cm^3 (Siau 1984). The percentage of volume occupied by water (V_{H_2O}) was calculated as

$$V_{H_2O} = \frac{(W_f - W_d) \times D_w}{V_f} \times 100,$$

where terms are defined as above for SG. The percentage of volume not occupied by either cell wall material or water was assumed to be occupied by air (V_{air}) and was calculated as

$$\left(1 - \left(V_{cell\,wall} + V_{H_2O}\right)\right) \times 100.$$

Xylem anatomy

Tracheid lengths and diameters were characterized for the second growth ring from the pith for all branch halves. An image analysis system consisting of a compound microscope, video camera, Quadra 800 Macintosh computer and NIH Image v. 1.60 (public domain software) was used to analyze both transverse sections and tracheid macerations.

Tracheid lumen diameter. Transverse sections of the proximal end of each half were made with a microtome, stained with safranin-O, mounted and viewed at 40x with the compound microscope. For the second growth ring of each branch half, inside-lumen diameters were calculated from measured lumen areas along three radial cell files. Transverse sections were visually divided into three sectors of equal area, and one radial file was randomly-selected from each. In this way we could observe radial trends in tracheid diameter across an entire annual ring. Frequency distributions of tracheid lumen diameters were used to calculate the contribution of each class (2μm increments) to total theoretical flow rate for each branch half. According to Poiseuille's law, the rate of fluid flow through a perfect capillary is proportional to the fourth power of the radius. While there are good reasons that measured flow rate is typically much less than theoretical flow rate (e.g., tracheids are not perfect capillaries, bordered pits add resistance), we use the calculations as a means of illustrating the potential hydraulic implications of different diameter distributions. In addition, the mean of the 5 largest earlywood tracheids was calculated for each branch half.

Tracheid length. Matchstick-sized wedges were removed from random positions within the second growth ring of each branch half and macerated in Jeffrey's solution (10% nitric acid and 10% chromic acid (1:1)) for approximately 4 hours (Berlyn and Miksche 1976). Macerations were rinsed, stained with safranin-O, mounted and viewed at 4x with the compound microscope. Lengths were measured for 150-250 randomly-selected tracheids per branch half.

Statistical analysis

Paired t-tests were used to test differences in hydraulic and anatomical parameters between branch halves. Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were used to test differences between the three branch ages with tree as a blocking factor. We use ANCOVA specifically to test for the significance of a covariate, percent compression wood, while controlling for the effect of sample diameter. All statistical procedures were conducted with Statistical Analysis Systems software (SAS Inc., 1996).

RESULTS

Whole branch segments

The hydraulic parameters k_s, k_h and LSC did not differ among the three branch ages (one-way ANCOVA with tree as a blocking factor, diameter as covariate, data not shown) and were therefore averaged for all 36 samples (Table 2.1). Compression wood occupied 18-60% of the sample cross-section (Table 2.1) but showed no relationship with either the diameter or angle of whole branch segments (data not shown). Neither Huber value, k_s (Figure 2.3), nor LSC (data not shown) were related to percent compression wood.

Branch halves

Upper and lower branch halves differed significantly in both hydraulic and anatomical properties (Table 2.2), and differed similarly for all three branch ages (one-way ANOVA

with tree as blocking factor, data not shown). Lower branch halves had less than 70% of the k_s of upper branch halves, and while they tended to be larger (the cross-sectional area of lower branch halves made up 52% $\pm$ 0.5 (mean $\pm$ se) of the total segment area), lower branch halves had consistently lower k_h values than upper branch halves (Table 2.2).

	Mean $\pm$ se	Minimum	Maximum
k_s (m^2 x 10^{-13})	8.1 $\pm$ 0.3	5.1	11.7
k_h (m^4 x 10^{-17})	4.3 $\pm$ 0.3	0.9	8.0
LSC (m^2 x 10^{-16})	1.42 $\pm$ 0.04	0.8	1.9
Huber value (x 10^{-4})	1.77 $\pm$ 0.04	1.3	2.2
Percent compression wood (%)	37 $\pm$ 2	18	60
Angle of segment (degrees)	64 $\pm$ 2	32	89
Diameter of segment (mm)	8.2 $\pm$ 0.2	4.9	10.7
Leaf area distal to segment (m^2)	0.30 $\pm$ 0.02	0.1	0.5

Table 2.1. Structural and hydraulic properties of branches and whole branch segments. Values shown are pooled for all three branch ages (n = 36).

Lower branch halves had significantly lower moisture contents and higher specific gravity than upper halves (Table 2.2). The proportion of total sample volume occupied by both cell wall material and air was greater for lower branch halves relative to upper halves, while the reverse was true for the volume occupied by water (Table 2.2). In order to prevent water loss prior to volume flow rate measurements, samples were stored in water and quickly surface-dried with a towel before weighing. Some water likely
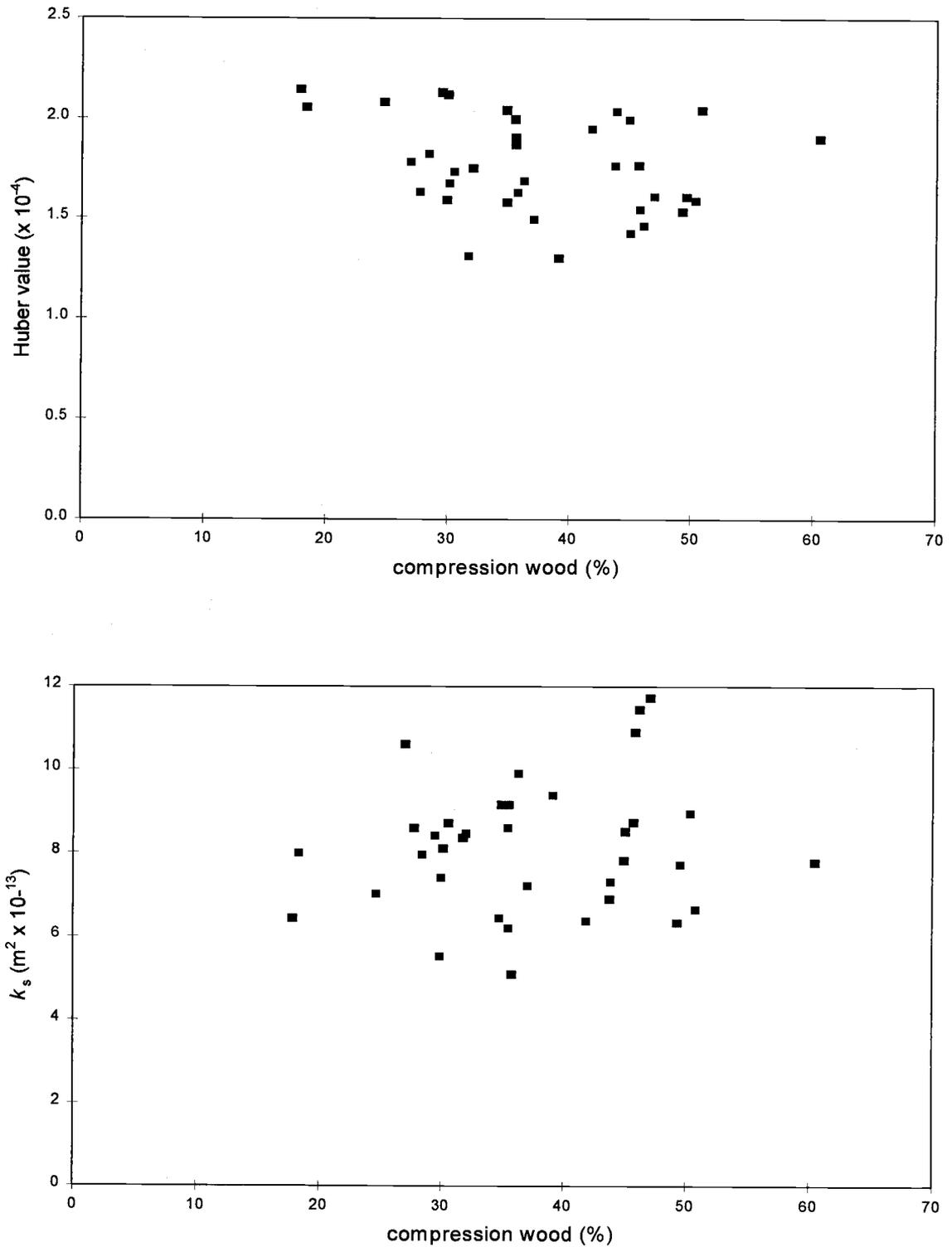
Figure 2.3. Huber value (sapwood area/distal leaf area) and k_s of whole branch segments vs. compression wood expressed as a percentage of sample cross-sectional area.

remained on the surface of samples and, as a result, the volume occupied by water is likely overestimated for both halves. The volume occupied by air is therefore underestimated. For some samples the calculated volumes of water and cell wall material summed to an amount greater than the fresh sample volume, producing negative values for air volumes.

While lower branch halves consistently had more cells within an annual ring, the cells tended to be shorter and, in the case of earlywood, smaller than cells in upper branch halves (Table 2.2). Within the second annual ring, the first-formed earlywood tracheids had the widest lumens for both branch halves, averaging 15 and 17 μm for lower and upper halves, respectively (Figure 2.4). Average lumen diameters of lower branch halves remained below those of upper halves for more than 70% of the annual ring width. Lower branch halves had a smaller range of tracheid diameters and a greater proportion of narrow tracheids than did upper halves (Figure 2.5). Based on calculated Σr^4 values, tracheids ≥ 16μm in diameter contribute only 29% of the total flow in lower branch halves, compared to over 60% in upper branch halves. (Figure 2.5).

Damage caused by splitting, as calculated from k_h for branch halves and whole branch segments, ranged from 0 to 36% with a mean (± se) of 12% ± 1.4. The smallest diameter samples were most affected by the splitting process (Figure 2.6).

		Upper branch half (UBH)	Lower branch half (LBH)	significance level[1]
Hydraulic properties				
	k_s (m^2 x 10^{-13})	9.3 ± 0.3	6.4 ± 0.3	***
	k_h (m^4 x 10^{-17})	2.2 ± 0.2	1.6 ± 0.1	**
Physical properties				
	specific gravity	0.45 ± 0.01	0.51 ± 0.01	***
	moisture content (%)	155 ± 3	123 ± 2	***
	$V_{cell\ wall}$ (%)	29.0 ± 0.3	33.0 ± 0.3	***
	V_{H2O} (%)	69.0 ± 0.7	62.0 ± 0.6	***
	V_{air} (%)	3.0 ± 0.7	5.0 ± 0.5	*
Anatomical properties				
	radial cell count	63 ± 2	73 ± 3	**
	EW tracheid diameter (μm)[2]	21.4 ± 0.4	18.6 ± 0.3	**
	mean tracheid length (mm)	1.4 ± 0.02	1.2 ± 0.01	**

Table 2.2. Hydraulic and anatomical properties of upper and lower branch halves. Means (± se) are shown for all three branch ages (n=36).

[1] Significance levels are based on paired t-tests performed separately for each branch age (n=12).
*** indicates a p-value < 0.0001
** indicates a p-value < 0.001
* indicates a p-value < 0.01

[2] Calculated as mean of 5 largest earlywood tracheids measured
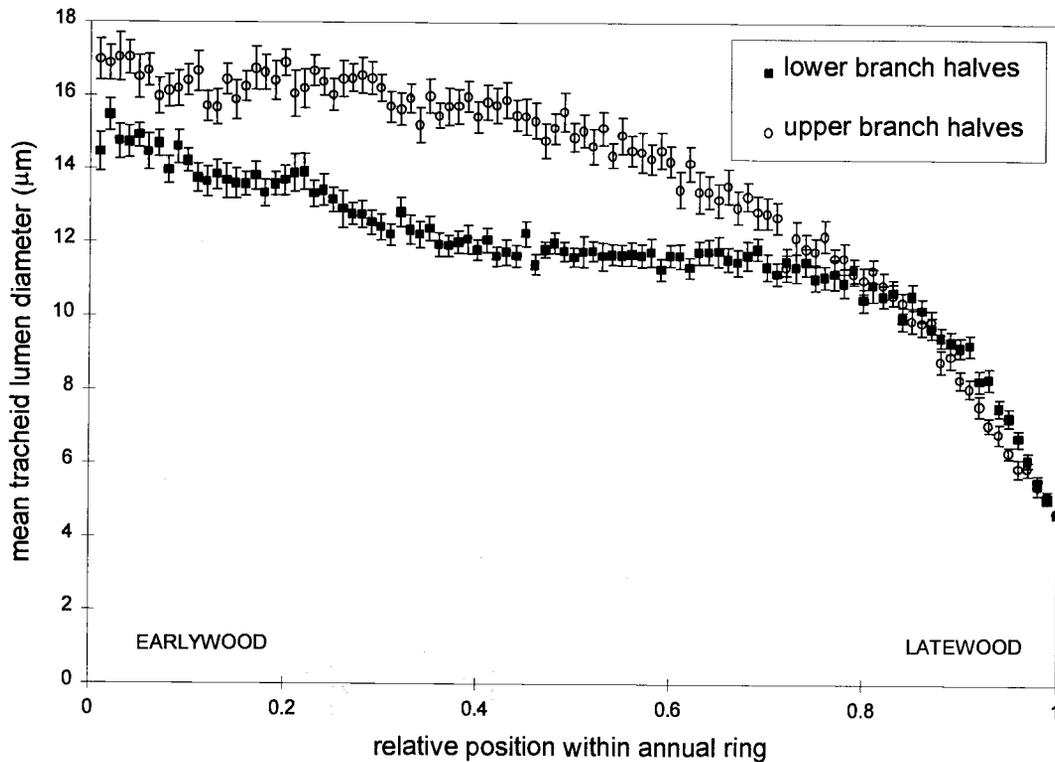
Figure 2.4. Trends in tracheid lumen diameter across the second annual ring for upper and lower branch halves. For each branch half, lumen diameters along 3 radial files were averaged by radial position. Each point represents the mean (error bars show se, n ranged from 29 to 35 depending on how many samples had a value for that position) of the average lumen diameter at that position for 36 branch halves.

DISCUSSION

We found strong evidence supporting the hypothesis that lower branch halves do, in fact, conduct water less efficiently than upper branch halves. Potentially, two aspects of xylem anatomy could compensate for the relatively impermeable compression wood in the lower portion of branches to produce upper and lower halves with equal hydraulic capacity. By having a sufficient number of large earlywood tracheids, lower branch halves could have the same k_s as upper halves. We found no evidence for this, as the k_s of
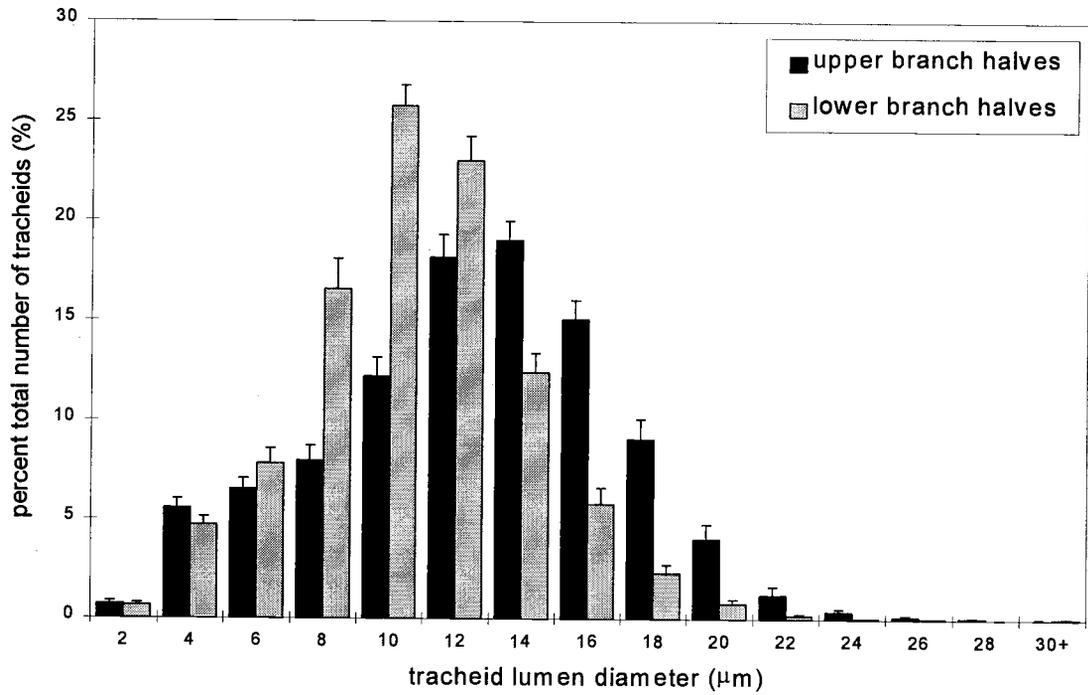
(a)
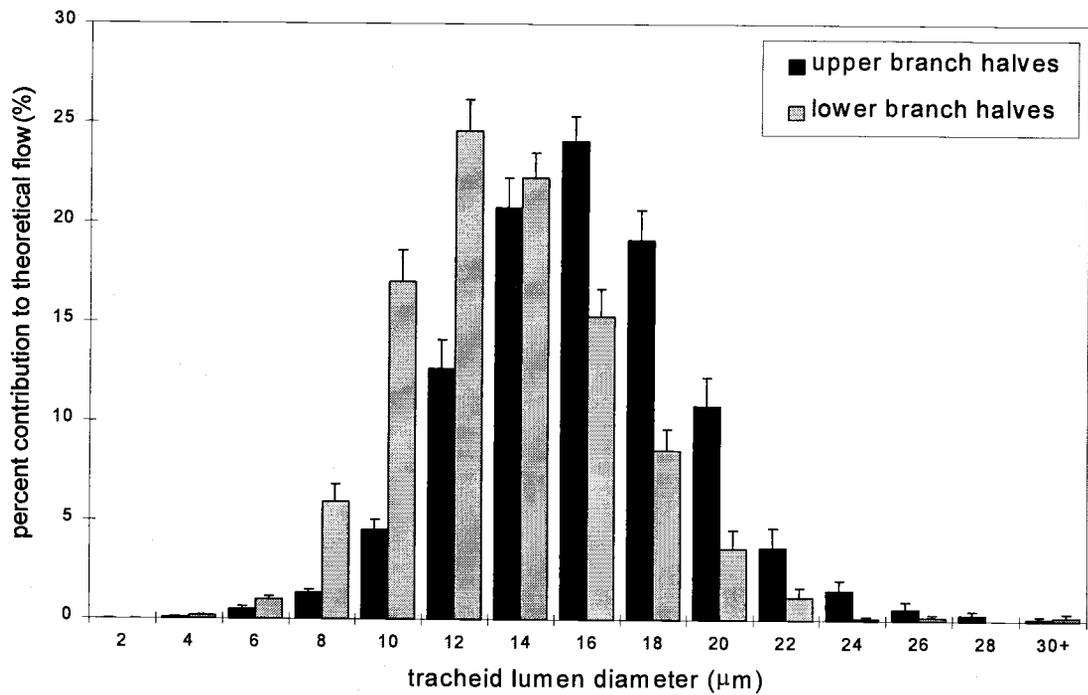
(b)

Figure 2.5. Frequency distributions of (a) tracheid lumen diameters and (b) the contribution of each diameter class to total theoretical flow based on Σr^4 values.

we observed up to 15 rows of normal earlywood tracheids in lower branch halves, even the largest of these were still significantly smaller than those of upper branch halves. This slight difference in the size of the largest cells likely contributes to the dramatic reduction in k_s for lower halves. For instance, tracheids 18-20μm in diameter made up roughly 2.5% and 9% of all cells measured, but contributed 8% and 20% to total theoretical flow for lower and upper halves, respectively. In addition to tracheid diameter, measured differences in tracheid length between halves could explain the low k_s of lower branch halves. Water must pass through bordered pit pairs to move from tracheid to tracheid in gymnosperms and pterophytes and this contributes significantly to the resistance to flow (Bolton and Petty 1978, Calkin et al. 1986, Gibson et al. 1985, Zimmermann and Brown 1971). Shorter tracheids found in lower branch halves would require more frequent passage through pit pairs, increasing resistance relative to upper halves. In addition to tracheary dimensions measured here, the size of pores in the membranes of bordered pits, the shape of the bordered pit aperture, and the frequency of pitting should all affect resistance to flow. In well-developed compression wood, like that found in the lower portion of branches, tracheids have fewer bordered pits on their radial walls and smaller pit apertures than those of normal wood (Lee and Eom 1988; Ohtani and Ishida 1981, as reviewed in Timell 1986).

The high specific gravity and low moisture content of lower branch halves are likely the result of large amounts of cell wall material relative to upper branch halves. In addition to having less overall void space (i.e., space not occupied by cell wall), lower halves had more void space occupied by air than upper halves. This could further reduce

the k_s of lower branch halves if the air were to occupy tracheids (Puritch 1971, Edwards and Jarvis 1982, Pothier et al. 1989, Sellin 1991). However, we did not find any relationship between air content and k_s, suggesting that the additional air in lower branch halves may occupy the intercellular spaces found in compression wood.

Despite the reduced permeability of lower branch halves, the amount of compression wood visible on the end of each sample did not explain any variation in hydraulic parameters (i.e., it was not a significant covariate, even after the inclusion of sample diameter in the model). This lack of relationship between LSC and percent compression wood suggests that the overall capacity of the xylem to supply foliage with water remains unaffected by the presence of compression wood in branches. How could a branch with 50% compression wood supply foliage with water as efficiently as a branch with 25% compression wood? One way would be to have an increase in conducting area per unit foliage (i.e., an increase in HV). We found no evidence for this, as HV remained relatively constant across a range of values for percent compression wood. The lack of relationship between whole sample k_s and percent compression wood suggests a second possibility. The formation of opposite wood in upper branch halves could compensate for lost conductive capacity due to compression wood. Many investigators have described opposite wood as having anatomy *opposite* that of compression wood (Park 1983, 1984a, b; Timell 1973a, b; Lee and Eom 1988), but none have studied it in the context of hydraulics. Disagreement in the literature regarding the dimensions of opposite wood tracheids, relative to those of compression wood, make it difficult to speculate on the hydraulic capacity of opposite wood (Nicholls 1982; Park 1983, 1984a, b; Lee and Eom 1988). However, if opposite wood were to counteract the hydraulic

effect of compression wood, one would expect the k_s of upper branch halves to increase and the k_s of lower branch halves to decrease with increasing percent compression wood. We did not find this to be the case. One final possibility is that the amount of compression wood visible in transverse section is a poor indicator of severity, and that severity, rather than amount, determines the effect on hydraulics. We were not able to separate the two effects in the current study. Indices describing severity, especially those based on the large earlywood tracheids (e.g., Harris 1976), may be useful in gauging the effect compression wood formation has on the efficiency of xylem transport.

The fact that percent compression wood was independent of both segment diameter and angle (i.e., angle of the segment within the branch, measured with respect to the vertical) underscores the complexity of compression wood formation in branches. Stems and branches have a predetermined equilibrium position (EP), such that movement out of this position stimulates compression wood formation that will return the shoot to its EP (Little 1967, Wilson and Archer 1974). In contrast to stems, in which deviation from the EP can be approximated by the angle of lean, deviation from the EP in branches is hard to assess (Timell 1986). Future work in compression wood hydraulics will require a more thorough treatment of branch mechanics in order to investigate the potential tradeoff between mechanical support and water transport functions of gymnosperm xylem. Given the importance of xylem efficiency to whole plant productivity and the relative impermeability of compression wood, more research is needed to determine the integrated effect of compression, opposite and lateral woods on whole shoot water relations.

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Chapter 3

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

Rachel Spicer and Barbara Gartner

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 test 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 the initial disparity in

hydraulic capacity between branches and leaders, and because of the large amount of

relatively impermeable compression wood that must form in branch-leaders during

reorientation of the shoot. By subsampling the basal portion of branch-leaders, we also

test the hypothesis that opposite wood (formed directly opposite compression wood) is

more permeable than normal wood (formed to the sides of compression wood), and could

therefore compensate for the presence of compression wood at the level of the whole

shoot. Fifteen months after leader removal, branch-leaders were intermediate between

branches and leaders in their ability to supply foliage with water, suggesting a transition

toward leader-status that was not yet complete. Increased hydraulic capacity in branch-

leaders was largely 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.

INTRODUCTION

The tops of trees 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; Ewers and Zimmermann 1984a, b; Tyree et al. 1983; 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 (Sellin 1987, Ewers and Zimmermann 1984a). 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 and 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 and Archer 1981, Wilson 1986). Does the branch assume the favored 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 (see Chapter 2) 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; Lee and Eom 1988; Park 1983, 1984a, b). 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 and Zimmermann 1984a).

In the current study, we explore answers to the questions listed above by studying the hydraulic properties of shoots in young Douglas-fir trees from which we removed the leader 15 months before, allowing a branch to move up in its place. By comparing the hydraulic properties of "branch-leaders" to those of intact leaders and branches, we describe the hydraulic transition from branch to leader. Specifically, we use 1- and 3-

year-old shoot segments to test the hypothesis that branch-leaders remain at a hydraulic disadvantage. 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 examine 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* (Mirb.) Franco) trees, ranging in age from 5 to 10 years, were selected randomly from a population of approximately 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" lat., 123°14'01" long., 136 m elev.), 10 km north of Corvallis, Oregon. In June of 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 three 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 of 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 above 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 introduced 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 about 5 cm long were excised near the base of both the 1- and 3-year-old portions of the shoot for each branch (B), branch-leader (BL) and leader (L). The bark was removed from each sample and the ends were shaved clean 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 weight, and subsampled in order to determine fresh area/dry weight 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 (L) and branch-leader (BL) segments; terminal shoot foliage for branch (B) segments; current-year, lateral shoot foliage for L and BL segments; 2- and 3-year-old, lateral shoot foliage for L and BL segments; all-ages of lateral shoot foliage for B segments. For each segment and foliar class, fresh needles were removed from 5 randomly-selected, 4 cm long sprigs and frozen until all conductivity measurements were made. The remaining foliage was dried in an oven for 48 hours at 60°C and weighed. The projected area (one side) of fresh foliage samples was determined using a video camera and NIH Image v. 1.52 (public domain software) on a Quadra 800 Macintosh. Samples were then dried and weighed to establish fresh area to dry weight ratios. Conversion ratios were used to calculate the amount of fresh leaf area distal to each segment for use in leaf-specific conductivity calculations (see below).

Specific conductivity. Specific conductivity (k_s) describes the permeability of a sample and is defined by Darcy's law as

$$k_s = \frac{Ql\eta}{A\Delta P},$$

where k_s is in m^2, Q is the volume flow rate (m^3/s), l is the length of the segment (m), η is the dynamic viscosity of the permeating fluid (1.008 x 10^{-3} Pa s (= N s m^{-2}) at 20°C, Jones 1992), A is the sapwood cross-sectional area (m^2), and ΔP is the pressure difference between the two ends of the segment.

Whole segments were fit with flexible tubing and a dilute solution of oxalic acid (10 mol/m^3, filtered to 0.22μm) was delivered to the distal end under a gravitational pressure head of about 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 et al. 1988, Zimmermann 1978). Fluid was collected from the proximal end for repeated periods of 1 min and weighed on an electronic balance. Volume flow rate was calculated as the mean of at least 5 collection periods. To determine dynamic viscosity, thermocouples were used to record the temperature of both the permeating fluid and the water in which samples were stored.

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

$$k_h = \frac{Ql\eta}{\Delta P},$$

where k_h is in m^4 and all terms are defined as above for k_s.

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

$$LSC = \frac{Ql\eta}{A\Delta P},$$

where LSC is in m^2, and all terms are defined as above for k_s, except A, which is defined as the sum of the leaf area (one side) both attached and distal to the segment. Huber value (HV) is defined as the ratio of xylem cross-sectional area to distal leaf area, and is therefore unitless. Note that

$$LSC = HV \times k_s.$$

Following conductivity measurements, whole segments (excluding 3-year-old branch-leaders segments, which were subsampled, see below) were perfused with filtered (0.22μm) 0.5% (w/v) safranin-O for 20 minutes. 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 sectioned longitudinally along their radii for further conductivity measurements. Preliminary tests showed that measuring volume flow rate twice on the same sample, with several hours between measurements, did not significantly affect the results. Three sectors (portion of a circle bounded by radii and the included arc) 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. The largest possible sector was drawn within each region to maximize the subsample cross-sectional area and minimize the damage caused by splitting (see Chapter 2). 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 (Figure 3.1).
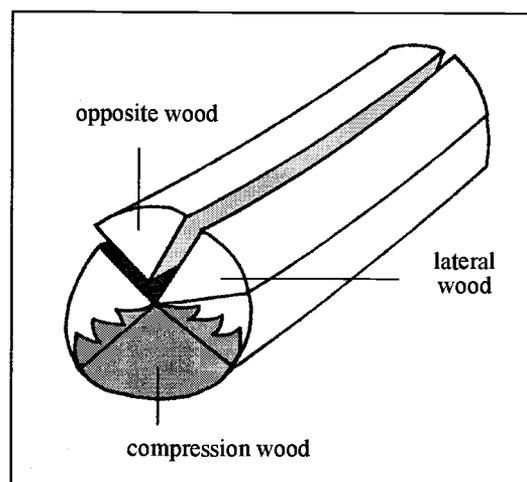
Figure 3.1. Location of opposite, lateral and compression wood subsamples.

Subsamples were sealed inside a pressure-sleeve apparatus (described below) for volume flow rate measurements. 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

$$A = \frac{r^2 \alpha}{2},$$

where r is the radius (mm) and α is the central angle in radians (1 radian = 360/(2Π)). The mean of r and α for the distal and proximal ends of each subsample were used.

Pressure-sleeve apparatus. Subsamples were enclosed in a modified pressure-sleeve apparatus (see Chapter 2) during conductivity measurements in order to seal the sides of the samples (Figure 3.2). A polyvinyl chloride (PVC) coupling devices was fit with a standard bicycle tube tire valve 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 Plexiglas® 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 center 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.
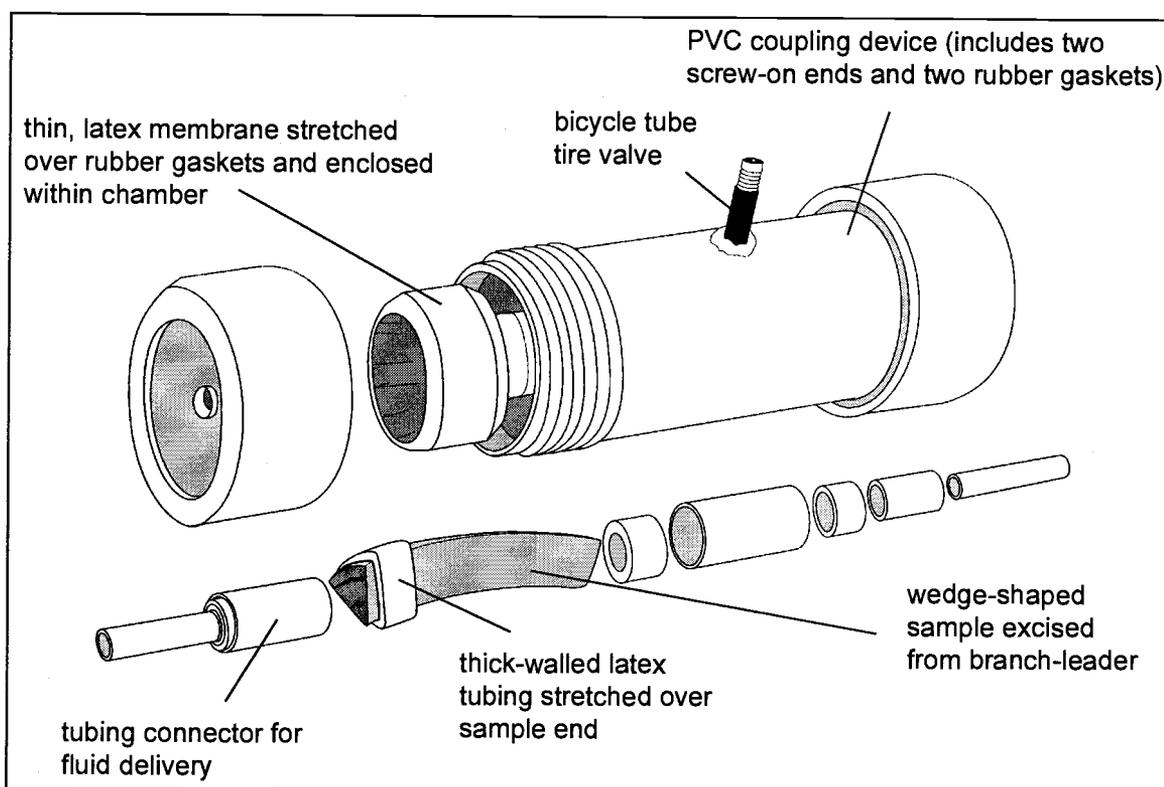
Figure 3.2. Pressure-sleeve apparatus and branch-leader subsample fit with connectors.

Subsamples were fit 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 (Figure 3.2). 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 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 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 and attached to the reservoir of oxalic acid (distal end), and to a 1 ml 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 0.01 ml intervals. The mean of at least eight timed intervals was used to calculate k_s.

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

Statistical analysis

Two-way analysis of variance (ANOVA) was used to compare same-age segments among shoot types (B, L, BL) and different ages within each shoot type. Treatment structure followed a factorial design with two ages nested within three shoot types. Tree pairs served as blocks. Differences between any two wood types (compression, opposite and lateral wood) subsampled from three-year-old branch-leader segment were tested with paired t-tests. All statistical procedures were conducted with Statistical Analysis Systems software (SAS Inc., 1996).

RESULTS

Whole shoot segments

Within each shoot type, 1-year-old segments had lower k_h but higher LSC and HV than 3-year-old segments (Table 3.1). 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.

		k_h (m^{4}x10^{-17})	k_s (m^{2}x10^{-13})	LSC (m^{2}x10^{-16})	distal leaf area (cm^2)	HV (x 10^{-4})
branch						
	age 1	1.0 ± 0.1[a]	10.3 ± 0.7[a]	5.7 ± 0.3[a]	170 ± 10[a]	5.8 ± 0.4[a]
	age 3	6.0 ± 0.5[b]	6.7 ± 0.5[b]	1.6 ± 0.1[b]	3970 ± 320[b]	2.4 ± 0.1[b]
branch-leader						
	age 1	4.2 ± 0.5[c]	9.2 ± 0.6[ca]	17.9 ± 1.3[c]	230 ± 23[c]	21.1 ± 2.2[c]
	age 3	23.4 ± 2.8[d]	6.7 ± 0.5[db]	3.4 ± 0.3[d]	6850 ± 590[d]	5.1 ± 0.2[d]
leader						
	age 1	5.1 ± 0.5[ec]	8.4 ± 0.6[ec]	26.9 ± 2.2[e]	210 ± 20[eca]	33.5 ± 2.7[e]
	age 3	101.9 ± 7.5[f]	15.1 ± 0.6[f]	8.0 ± 0.6[f]	13150 ± 970[f]	5.3 ± 0.3[fd]

Table 3.1 Hydraulic and foliar properties for each shoot type and segment age (mean ± se, n = 15). Within each column, means with the same letter did not differ significantly at the 0.05 level (two-way ANOVA with nested treatments, tree pair as block).

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 was higher in branches than in leaders, but otherwise 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 (HV, 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, HVs of 3-year-old leader and branch-leader segments were similar but significantly higher than those of 3-year-old branch segments. LSCs of 1- and 3-year-old segments followed a pattern identical to that of HV 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 LSC (Figure 3.3). 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 LSCs 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.
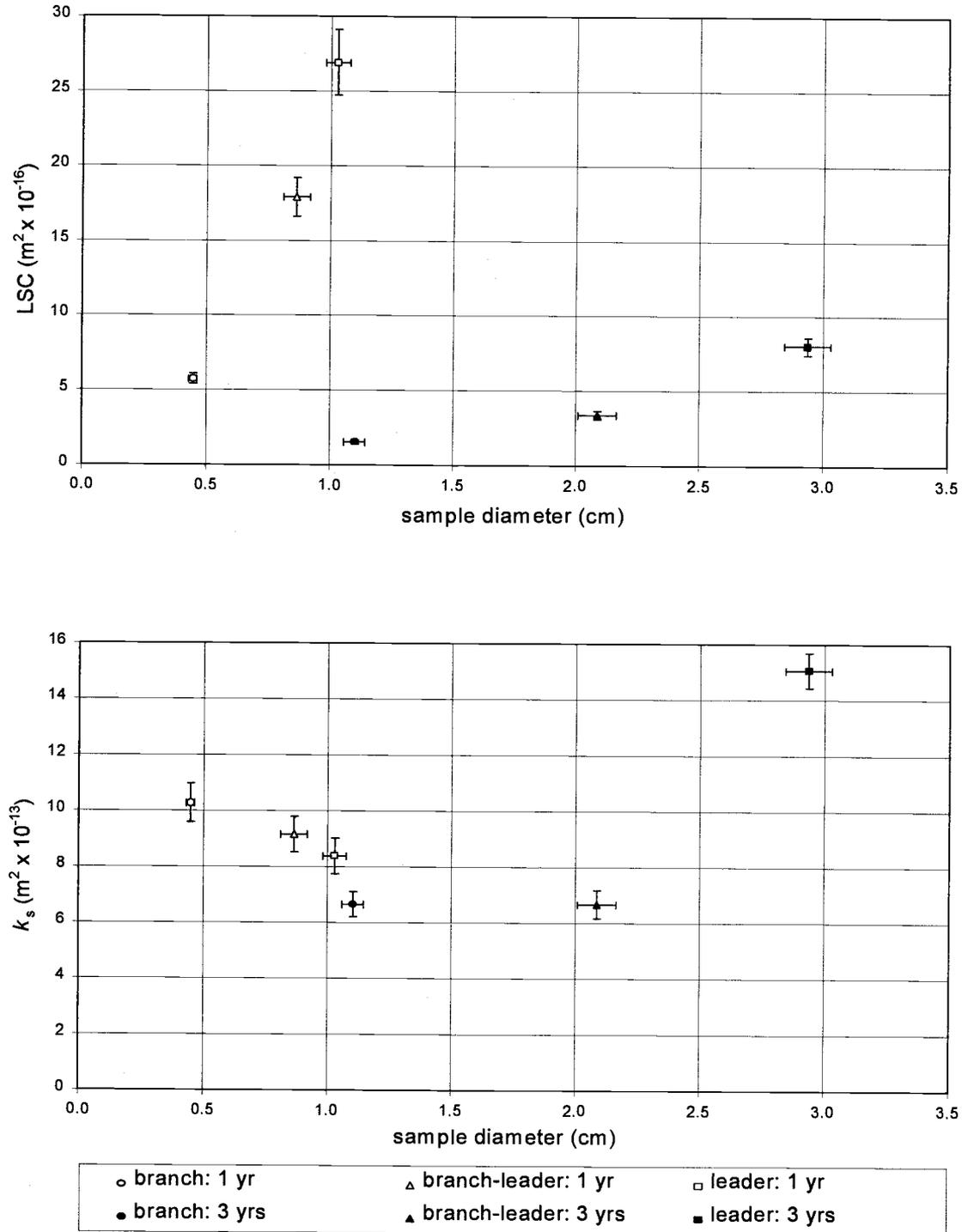
Figure 3.3. Mean k_s and LSC as a function of mean sample diameter (n=15). Symbols represent means, error bars show standard error for k_s, LSC (vertical) and diameter (horizontal). Open symbols represent 1-year-old segments; closed symbols represent 3-year-old segments. Circles represent branches; squares represent leaders; triangles represent branch-leaders.

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 3.2). Compression and opposite wood had, respectively, 21 ± 3 and 65 ± 7% (mean ± 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.

	compression wood	opposite wood	lateral wood
k_s (m^2 x 10^{-13})	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 3.2. Specific conductivity (k_s, m^2 x 10^{-13}) and dimensions of subsamples from regions of compression, opposite and lateral wood within 3-year-old branch-leader segments (mean ± se, n=15). Within each row, means with the same letter were not significantly different at the 0.01 level (differences between any two wood types based on paired t-tests).

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 LSC 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 and Pockman 1993, Sperry et al. 1993).

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

Differences in LSC among 1-year-old segments were the result of differences in HV rather than in k_s. In the case of leaders, the HV was large enough to overcome a k_s lower than that of branches. In other words, 1-year-old leaders a maintained higher LSC than branches, despite lower xylem permeability, by producing more xylem area per unit foliage. The high LSC of 1-year-old branch-leaders relative to branches can also be attributed to a high HV, as the two shoot types had similar k_s.

Differences in LSC among 3-year-old segments were the result of more complex interactions. Leaders and branch-leaders had very similar HVs but differed in k_s: in this case, the high LSC 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 HV: the high LSC of the branch-leader is the result of a larger conducting area per unit foliage. This increase in HV occurred despite a nearly two-fold increase in foliage for branch-leaders over that

of branches. The high LSC of 3-year-old leader segments in relation to branch segments can be attributed to both a high k_s and HV.

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 both toward both the tip and base (Ewers and Zimmermann 1984a, b; Sellin 1987, 1988, 1994). While 3-year-old segments came from the most basal region of branches and branch-leaders, they came from a region relatively near the top of the main axis in the case of leader segments. This axial change in k_s results from developmental changes in tracheary dimensions (Duff and Nolan 1953, Dinwoodie 1961, Larson 1969, Megraw 1985, Aloni 1987). While the decrease in tracheid size toward the tip of a trunk or branch is the result of a decrease in cambial age, the cause of the decrease observed toward the base may differ between shoot types (Panshin and de Zeeuw 1980, Zobel and van Buijtenen 1989). It is not known to what extent compression wood is responsible for the decline in k_s toward the base of branches.

Among 1-year-old segments, branches had higher k_s than leaders, while the reverse was true for 3-year-old segments. This pattern has also been observed in *Abies balsamea* (Ewers and 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 differ in the first ring

from the pith but increase rapidly moving toward the bark (Park et al. 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). Among 1-year-old segments in this experiment, compression wood was more frequent in leaders and branch-leaders than in branches, which could account for their low k_s relative to branches.

It is not possible to tell from the current study whether the lower LSC of 3-year-old segments from branch-leaders relative to those of 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 is 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 and 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 several more years of xylem production (possibly just one), the basal region of branch-leaders will have the same LSC as intact leaders. In contrast, it is surprising that 1-year-old branch-leader segments, which had no special mechanical requirements, had lower LSCs (attributable entirely to lower HVs) than those of leaders. It may be that new branch-leader growth (produced entirely in the absence of a leader) is limited by xylem transport efficiency of more basal regions. Further research is needed to improve our understanding of the hydraulic impact of the mechanically-specialized compression wood.

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Chapter 4

Conclusion

THE IMPACT OF COMPRESSION WOOD ON XYLEM TRANSPORT EFFICIENCY

The xylem of plant stems typically functions in both mechanical support and water transport, and evidence here (Chapters 2 and 3) suggests that these two functions have conflicting structural requirements. Xylem that develops in the absence of mechanical requirements (e.g., lianas; staked, guyed or otherwise externally-supported stems) is typically more permeable than xylem that develops in self-supported stems (Dean 1991, Gartner 1991). Similarly, compression wood, which is specialized to function in mechanical support, has been shown here to be less permeable than normal wood in branches (Chapter 2) and reoriented shoots (Chapter 3) of Douglas-fir (*Pseudotsuga menziesii*). It is not surprising that xylem specialized for mechanical support has limited efficiency in water transport. Lower branch halves in Douglas-fir contained large amounts of compression wood, and as a result had higher specific gravity (owing to large amounts of cell wall material), and shorter and narrower tracheids than upper branch halves. The connection between xylem anatomy and permeability is well-known, and all of the characteristics listed above have been associated with reduced hydraulic capacity (Booker and Kininmonth 1978; Ewers and Zimmerman 1984a, b; Pothier et al. 1989; Sellin 1990; Coyea and Margolis 1992).

Xylem variation affects water transport at a number of scales, ranging from within a single annual ring, to within and among individuals, species and higher taxa. Most

work in xylem transport, particularly in gymnosperms, has occurred at the level of the

organ (e.g., branch, root, stem) or higher. To further our understanding of compression

wood and its impact on xylem transport, it is necessary to operate at a level below the

whole organ and consider the integrated effect of different types of xylem within a shoot.

Although the anatomy of "pure" compression wood should (and *does*) increase resistance

to the flow of water, there are a number of ways in which anatomy at the whole shoot

level could counteract compression wood, producing no observable effect for the cross-

section as a whole. Evidence for several of these compensatory mechanisms was lacking

in Douglas-fir shoots and branches. The eccentric growth associated with compression

wood (i.e., the increased cross-sectional area available for transport) and the production

of large, seemingly normal earlywood cells were not sufficient to afford lower branch

halves the same permeability as upper halves. In addition, the low permeability of

opposite wood relative to normal wood in reoriented shoots suggests that *it* does not

compensate for lost hydraulic efficiency due to compression wood. The apparent

contradiction that branch segments with varying amounts of compression wood were

equal in their ability to supply foliage with water deserves further attention.

The work here in Douglas-fir highlights important functional differences, both

hydraulic and mechanical, between branches and main stems (leaders). In accordance

with a large body of literature (e.g., Zimmermann 1984a, Sellin 1987), main stems

supplied foliage with water more efficiently than lateral branches. As a result, the

transition from branch to leader required significant structural changes, including an

increase in cross-sectional area per unit foliage. This increase was large enough to

counteract (and at least partially overcome) the reduced permeability resulting from both

a core of branch wood and a large amount of compression wood. The very process of shoot reorientation during the transition from branch to leader illustrates a second, critical functional difference: the EP, or equilibrium position (Little 1967, Wilson 1973, Wilson and Archer 1974). The orthotropic habit of main stems means that their EP is vertical. Displacement from the EP then requires the action of an external force (e.g., wind, snow, falling trees, curious scientists). In contrast, the plagiotropic habit of branches means that their EP is at some angle with the vertical, and displacement occurs every year with new growth and increasing self-weight, in addition to external factors. Given that displacement from the EP is the norm in branches, it seems plausible that branches will differ from leaders in both the pattern of development and hydraulic impact of compression wood. One developmental difference is already known: the eccentric growth associated with compression wood formation in branches is minimal compared with that in main stems (Timell 1986). It may be that compression wood formation affects water transport quite differently in branches and main stems.

The removal of the leader in treated trees caused, in essence, a sudden change in the EP of one or more adjacent lateral branches. Although not directly comparable, differences in permeability between lower branch halves and compression wood in branch-leaders suggest a potential difference in the hydraulic impact of compression wood between two levels of displacement from the EP. Lower branch halves, composed largely of compression wood but also containing some lateral wood, had about 70% of the permeability of upper halves. Wide bands (up to 15 rows) of thinned-walled earlywood tracheids were observed at the start of the annual ring before the appearance of thick-walled compression wood cells. In contrast, "pure" compression wood taken from

branch-leaders had about 30% and 20% of the permeability of opposite and lateral wood, respectively. Preliminary anatomical analyses (not included here) show branch-leader compression wood samples to have only one or two rows of thinned-walled cells before the appearance of thick-walled compression wood cells. This distinction between the mild, normal displacement from the EP occurring annually in branches, and the severe, abnormal displacement occurring in stems is an important one. While it is tempting, particularly in terms of experimental design, to purposely reorient shoots in order to study the development (and hydraulic impact) of compression wood, it may not address the real question of how a tree functions normally. The response of a branch (i.e., compression wood formation) to a sudden, radical, or prolonged displacement from its equilibrium position may be quite different from the response to the gradual increases in self-weight experienced annually.

AREAS FOR FUTURE RESEARCH

To further our understanding of the role of compression wood in plant water relations, rather than its effect on xylem transport alone, studies need to be conducted at the whole plant and leaf level. Does a large amount of compression wood lower whole plant conductance? Do low levels of compression wood formation, like those in sinuous leaders, affect xylem transport efficiency? Are the xylem tensions generated in otherwise comparable individuals greater in individuals containing compression wood? Can the presence of compression wood reduce conductance to the point of causing early stomatal

closure and thereby limit gas exchange? These questions are important, not only to the field of physiological ecology, but also from a productivity standpoint.

A better understanding of the relationship between mechanical and water transport functions of the xylem is also worth pursuing. It is unlikely that there is a simple answer to the question "is there a tradeoff between xylem mechanical and hydraulic functions?" Instead, questions more restricted in scope must be asked. Does the amount of compression wood in branches affect the amount of foliage they are able to support? Is a stem displaced from the vertical at a hydraulic disadvantage as a result of compression wood formation? Do stems and branches differ in the degree to which their hydraulic capacity is affected by compression wood? Studies integrating both biomechanical and hydraulic techniques should shed light on how plants produce xylem designed to meet both functional requirements.

The righting action of compression wood illustrates the amazing plasticity required of organisms as long-lived as trees. It is clearly worth investigating how organs, individuals and species are affected by associated "costs". Although one form of hydraulic cost has been shown here, there may be mechanisms that allow xylem formation to compensate for the presence of impermeable compression wood. Even so, such mechanisms may carry a carbon cost (e.g., production of greater cross-sectional conducting area in the presence of compression wood). Ultimately, investigations must consider how compression wood affects whole plant resource allocation.

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