Spring and summer hydraulic conductivity of 14 woody species of the sub-boreal forest in British Columbia

Jian R. Wang

Abstract: Four hydraulic properties of the xylem, the Huber value (HV), hydraulic conductivity (K_h), and specific (K_s) and leaf-specific hydraulic conductivity (K_l) were studied during the spring before leaf-out and during the summer after full leaf-out for 14 co-occurring tree and shrub species in the sub-boreal mixedwood forests of central British Columbia. The 14 studied species were divided into deciduous and evergreen angiosperm and gymnosperm groups, including one deciduous gymnosperm species, the tamarack, *Larix laricina* (Du Roi) K. Koch. I tested whether species with different life forms and classification divisions have different hydraulic properties. HVs were statistically similar for all angiosperms but significantly different among gymnosperms. Long-lived, late-successional species had higher HVs than pioneer and early-successional species. K_s and K_l values for all species except one, subalpine fir, *Abies lasiocarpa* var. *lasiocarpa* (Hook.) Nutt., were significantly higher in the spring than in the summer. Conductivity was higher in angiosperms than in gymnosperms in both the spring and the summer, and was highest in deciduous species in both seasons. The results indicate that requirements for mechanical strength may account for the high HVs in conifers, and that the high HVs compensate for low K_s and K_l values. The high hydraulic conductivities observed in the spring coincide with high water availability and high water demand by trees with emerging leaves. The subsequent reduction in K_s and K_l values could be caused by drought-induced embolism and cavitation in early summer.

Résumé : Les propriétés hydrauliques du xylème : la valeur de Huber, la conductivité hydraulique (K_h), la conductivité hydraulique spécifique (K_s) et la conductivité hydraulique spécifique du feuillage (K_l), ont été étudiées au printemps avant que les feuilles sortent et pendant l'été après la fin de la foliation chez 14 espèces d'arbres et arbustes présentes ensemble dans les forêts sub-boréales mélangées du centre de la Colombie-Britannique. Les 14 espèces étudiées ont été divisées sur la base de leur feuillage, caduc ou persistant, et selon qu'elles appartiennent au groupe des gymnospermes ou à celui des angiospermes incluant une espèce de gymnosperme à feuillage caduc, *Larix laricina* (Du Roi) K. Koch. Les auteurs ont testé si les espèces appartenant à différents types biologiques ou à différentes divisions de la classification ont des propriétés hydrauliques distinctes. La valeur de Huber était semblable pour toutes les angiospermes mais significativement différente parmi les gymnospermes. Les espèces longévives de fin de succession avaient des valeurs de Huber plus élevées que les espèces pionnières et les espèces de début de succession. La conductivité hydraulique spécifique et la conductivité hydraulique spécifique du feuillage de toutes les espèces à l'exception d'une, *Abies lasiocarpa* (Hook.) Nutt., étaient significativement plus élevées au printemps qu'à l'été. Les angiospermes avaient une conductivité hydraulique plus élevée que les gymnospermes tant au printemps qu'à l'été. La conductivité hydraulique était la plus élevée chez les espèces à feuillage caduc durant les deux saisons. Les résultats indiquent que les exigences associées à la résistance mécanique peuvent expliquer les valeurs de Huber élevées chez les conifères et que ces valeurs élevées compensent pour les faibles valeurs de K_s et K_l. La conductivité hydraulique élevée observée au printemps coïncide avec la période de disponibilité élevée et de forte demande en eau chez les arbres dont les feuilles commencent à sortir. La réduction subséquente des valeurs de K_s et K_l pourrait être causée par des phénomènes d'embolie et de cavitation provoqués par la sécheresse au début de l'été.

[Traduit par la Rédaction]

Introduction

Hydraulic conductivity of woody plants can be linked to their potential growth rates and competitive abilities (Bond 1989; Tyree 2003). The hydraulic architecture of trees has been reviewed recently (Cruiziat et al. 2002; Tyree and Zimmermann 2002) and compared between gymnosperms and angiosperms (Patiño et al. 1995; Becker et al. 1999). Gymnosperms have lower specific hydraulic conductivity (K_s) than angiosperms because tracheids are smaller and less conductive than vessels. Woody plants vary in their capacity to conduct water, and in their vulnerability to embolism (Wang et al. 1992; Vander Willigen and Pammenter 1998; Becker et al. 1999; Sparks and Black 1999). Larger vessels, while allowing greater water flow, have typically been associated with higher vulnerability to embolism and cavitation, whereas small-diameter vessels and tracheids are more resistant to

Received 1 September 2004. Accepted 2 August 2005. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 22 November 2005.

J.R. Wang. Faculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7A 5E1, Canada (e-mail: jian.wang@lakeheadu.ca).

 doi: 10.1139/X05-176 © 2005 NRC Canada

Table 1. The 14 major woody tree and shrub species investigated.

Scientific name	Code	Common name	Class[a]	Leaf habit[b]
Cornus stolonifera Michx.	Cs	Red dogwood	A	D
Viburnum edule (Michx.) Raf.	Ve	Highbush cranberry	A	D
Amelanchier alnifolia (Nutt.) Nutt.	Aa	Saskatoon-berry	A	D
Betula papyrifera Marsh.	Bp	Paper birch	A	D
Lonicera involucrata Banks ex Spreng.	Li	Black twinberry	A	D
Salix spp.	Sa	Willows	A	D
Populus tremuloides Michx.	Pt	Trembling aspen	A	D
Alnus viridis subsp. *sinuata* (Regel) A. & D. Löve	Av	Sitka alder	A	D
Populus trichocarpa Torr. & Gray	Ptr	Black cottonwood	A	D
Larix laricina (Du Roi) K. Koch	Ll	Tamarack	G	D
Abies lasiocarpa var. *lasiocarpa* (Hook.) Nutt.	Al	Subalpine fir	G	E
Pseudotsuga menziesii var. *glauca* (Beissn.) Franco	Pm	Douglas-fir	G	E
Pinus contorta var. *latifolia* Engelm.	Pc	Lodgepole pine	G	E
Picea glauca (Moench) Voss	Pg	White spruce	G	E

[a]A, Angiospermae; G, Gymnospermae.
[b]D, deciduous; E, evergreen.

water flow and embolism (Wang et al. 1992; Pallardy et al. 1995; Davis et al. 1999; Tognetti et al. 1999). It is also well known that in addition to drought, freeze–thaw cycles in winter can cause embolism and loss of conductivity in many species (Zhu et al. 2000), with conifers typically being less affected than broadleaf species (Wang et al. 1992; Davis et al. 1999).

For an individual tree, total leaf area is closely correlated with the cross-sectional area of the water-conducting portion (sapwood) of the main stem (Waring et al. 1982; Enquist et al. 1998; Enquist and Niklas 2002). The Huber value (HV), which is a measure of the sapwood investment made by a plant in order to supply its leaves with water, relates the plant's sapwood area to its leaf area (sapwood cross-sectional area : unit leaf area; $cm^2 \cdot cm^{-2}$). HVs for woody plant species are variable and adaptive (Mencuccini and Grace 1995; Maherali and DeLucia 2001), especially in pines (DeLucia et al. 2000). However, they are relatively constant among ponderosa pine, *Pinus ponderosa* Laws., of different ages (O'Hara and Valappil 1995). The efficiency of that sapwood to conduct water also then becomes of interest and must be considered, along with the mechanical characteristics and successional status of the tree. Comparisons can be made between competing individuals growing in a mixed forest, to gain a better understanding of the relationships between leaf area, sapwood area, HV, K_s, and leaf-specific hydraulic conductivity (K_l) across species and leaf habits.

There has not yet been a comprehensive study comparing the hydraulic characteristics of co-occurring, competing species at the same site at different times of the year (i.e., before and after leaf-out), and a study of this type is required to elucidate possible relationships between leaf area, sapwood area, HV, and hydraulic conductivity across species or classes (angiosperms, gymnosperms), as well as within growth habit and successional status (Becker et al. 1999).

To gain a more complete understanding of the hydraulic relationships of woody plants in different seasons, it would be of interest to investigate whether the HVs and K_s, and K_l values for angiosperms and gymnosperms are significantly different. Is there a correlation between successional status and HV, K_s, and K_l? Within a class (Angiospermae and Gymnospermae) or leaf habit (deciduous and evergreen), are there significant differences between HV, K_s, and K_l? Are there relationships between leaf area and sapwood area and HV, and between K_s and HV, across species?

The objectives of this study were to determine and compare the HVs and K_s and K_l values for 14 major tree and shrub species (Table 1) in sub-boreal forests in central British Columbia. Specifically, I tested the following hypotheses: (*i*) HVs and K_s and K_l values are statistically different between gymnosperms and angiosperms; (*ii*) they are different within gymnosperms but not significantly different within angiosperms.

Materials and methods

Study site and plant material

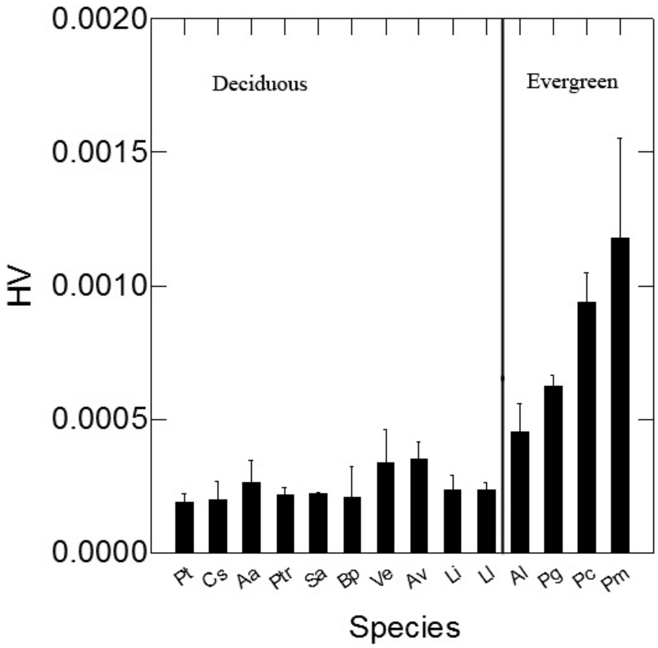
Branch samples were collected from mature sub-boreal mixed-species forests around Prince George (53°45′N, 122°42′W, elevation 620 m asl) in the centre of British Columbia. Normal, undamaged branches or stems (leafless in the case of deciduous species) about 1 cm in diameter were cut from young woody trees and shrubs belonging to 14 species (Table 1), labelled, and immediately placed in a bucket containing tap water. For each species, three stems were collected from different individuals randomly selected in the forests. The stems were kept hydrated in a refrigerator at 1 °C, and all hydraulic-conductivity measurements were performed within 2 days after collection.

Hydraulic conductivity

Two sets of measurements were carried out during 2000, one in April before bud break and a second one during June after leaves of all species had fully developed. K_h was measured according to the method described by Sperry et al. (1988) and Wang et al. (1992). Branch samples were measured in completely random order. Each branch sample (>1 m long) was immersed, then cut and trimmed to a 10 cm long segment with a sharp razor under water in a large tank filled with filtered (0.5 µm activated carbon/ceramic filter) acidi-

© 2005 NRC Canada

Fig. 1. Huber values (HV; mean ± 1 SE, n = 3) for 14 woody species of sub-boreal forests in central British Columbia in the summer, divided into deciduous and evergreen groups. For species' name codes see Table 1.



fied water to prevent microbial growth in the system. This process was designed to avoid introducing air emboli into the cut end of the segment. The segments (3 for each set) were attached to a system of tubing where K_h was measured at a regulated pressure of 2–5 kPa. Stem efflux was collected in a container and weighed using a balance connected to a laptop computer through the software Winwedge (version 3, TAL Technologies, Inc., Philadelphia, Pennsylvania). The efflux weight was recorded automatically every 30 s.

K_h (kg·m^{-1}·s^{-1}·kPa^{-1}) was calculated as the volume flow rate divided by the pressure gradient. K_s (kg·m^{-1}·s^{-1}·kPa^{-1}) was calculated as K_h divided by the stem cross-sectional area of the segment, and K_l (kg·m^{-1}·s^{-1}·kPa^{-1}) was calculated as K_h divided by total leaf area on that branch above the final cut point. After hydraulic conductivity was measured, stems were perfused with filtered (0.2 μm) 0.01 basic fuschin solution under hydrostatic pressure to determine the functional xylem area of each segment. Dye infiltration showed that the entire stem was composed of functional xylem. Therefore, stem cross-sectional area (excluding bark) (Davis et al. 1999; Kavanagh et al. 1999; Lemoine et al. 1999) was used as sapwood area in calculating the various parameters.

Leaf area and sapwood area

No leaf-area data were available for deciduous species collected in April, therefore leaf area was not measured on the conifer stems collected at that time. For each stem collected in June, all leaves distal to the base of the segment used to measure conductivity were removed without the petioles or fascicles. The leaf areas of broadleaf species were measured using a LI-3100 leaf-area meter (LI-COR, Inc., Lincoln, Nebraska). The projected leaf areas of coniferous species were determined on a subsample of needles from each stem, using a flatbed scanner and WinSeeddle software (version 4.5, Régent Instruments Inc., Québec, Quebec). The total leaf area of each branch was calculated from the specific leaf area.

Statistical analysis

The data were checked for normality using the univariate procedure (Shapiro–Wilk test) in SAS® (version 6.12, SAS Institute Inc., Cary, North Carolina). The statistical model for ANOVA of K_s included species, time, and the interaction term between species and time as sources. K_l and HV were only determined in the summer, therefore time was dropped from the model for ANOVA of these variables. General Linear Models was used to perform ANOVAs on HV, K_s, and K_l to test for significant differences among species, between spring and summer, and between gymnosperms and angiosperms. Three planned contrasts were performed: (1) a test for significant differences in K_s, K_l, and HV values between gymnosperms and angiosperms, (2) a test to determine whether the deciduous conifer *Larix laricina* (Du Roi) K. Koch (tamarack) differed significantly from the other deciduous species; and (3) a test to determine whether tamarack differed significantly from the other evergreen coniferous species.

Results

Huber values (HV)

No leaf-area data were obtained in the spring (no leaves in the case of deciduous species), therefore HVs were only calculated from the summer measurements. The mean HVs for the two life forms (deciduous and evergreen) were significantly different from each other (P = 0.0001) (Fig. 1). Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) exhibited a mean HV of 1.18×10^{-3}, the highest of all species, while trembling aspen (*Populus tremuloides* Michx.) had the lowest value, 1.91×10^{-4}. The mean HV for interior Douglas-fir was more than four and a half times that for the angiosperms. When testing for significant differences in HV within each life form, it was found that the deciduous species did not vary significantly in their HVs (P = 0.5242), while the evergreen species showed very significant differences (P = 0.0001; Fig. 1). No significant difference was found (P = 0.9939) when the HV for tamarack, a deciduous conifer, was compared with the HVs for the other deciduous broadleaf species. The HV for tamarack did, however, differ significantly from those for the other conifers (P = 0.0004). All the HVs for the broadleaf species were between 1.91×10^{-4} and 3.48×10^{-4}, while those for the conifers ranged from 2.36×10^{-4} to 1.18×10^{-3} (Fig. 1).

Leaf-specific hydraulic conductivity (K_l)

K_l values were only calculated from the summer data set, as the deciduous species are leafless in the spring. Significant differences in K_l values were found between deciduous and evergreen species (P = 0.0001; Fig. 2). Also, K_l values differed significantly among species within the deciduous group (P = 0.0001). In contrast, evergreen species did not differ significantly in their K_l values (P = 0.7539). It was found that tamarack had a K_l value that was significantly different from those for broadleaf deciduous species (P = 0.0001) but not from those for the other conifers (P = 0.4429; Fig. 2).

© 2005 NRC Canada

Fig. 2. Leaf-specific hydraulic conductivity (K_l; mean ± 1 SE, n = 3) of 14 woody species of sub-boreal forests in central British Columbia in the summer, divided into deciduous and evergreen groups. For species' name codes see Table 1.

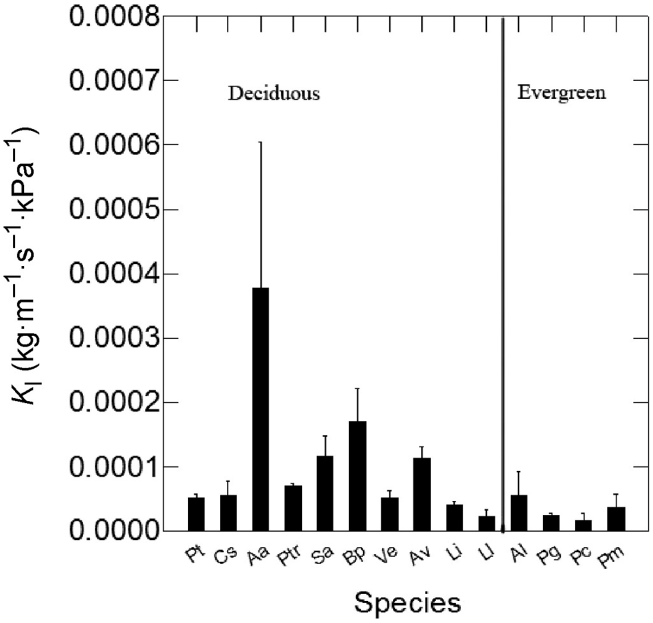
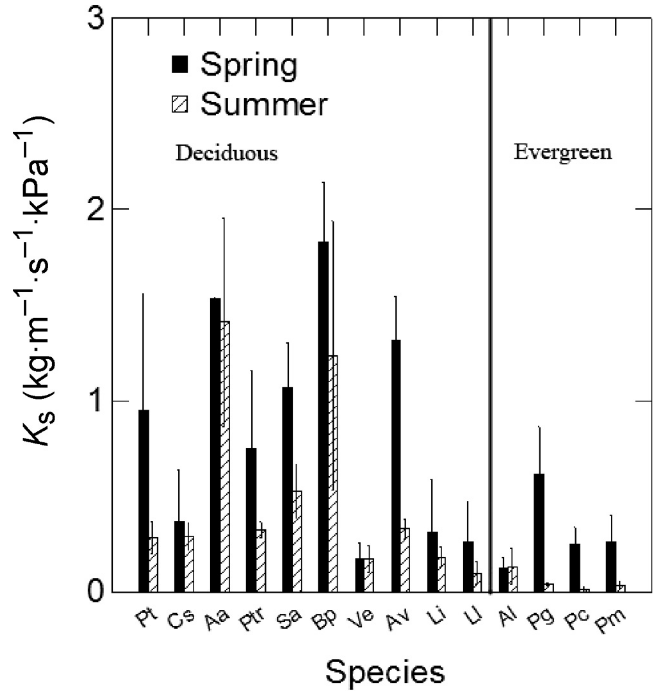


Fig. 3. Specific hydraulic conductivity (K_s; mean ± 1 SE, n = 3) of 14 woody species of sub-boreal forests in central British Columbia in the spring and summer, divided into deciduous and evergreen groups. For species' name codes see Table 1.



Saskatoon-berry (*Amenlanchier alnifolia* (Nutt.) Nutt.) exhibited the highest mean K_l value of all species (3.76×10^{-4} kg·m^{-1}·s^{-1}·kPa^{-1}), while lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) had the lowest (1.64×10^{-5} kg·m^{-1}·s^{-1}·kPa^{-1}) (Fig. 2). The evergreen species with the highest mean K_l value was subalpine fir (*Abies lasiocarpa* var. *lasiocarpa* (Hook.) Nutt.), with a value of 5.51×10^{-5} kg·m^{-1}·s^{-1}·kPa^{-1}, while the deciduous species with the lowest mean K_l value was black twinberry (*Lonicera involucrata* Banks ex Spreng.) (4.01×10^{-5} kg·m^{-1}·s^{-1}·kPa^{-1}).

Specific hydraulic conductivity (K_s)

K_s values were higher in the spring than in the summer for all species except subalpine fir, which had slightly higher value in the summer (Fig. 3). The species that exhibited the highest K_s value in the spring was paper birch, *Betula papyrifera* Marsh. (1.83 kg·m^{-1}·s^{-1}·kPa^{-1}), while the species with the lowest K_s value was subalpine fir (0.124 kg·m^{-1}·s^{-1}·kPa^{-1}) (Fig. 3). Saskatoon-berry had the highest summer K_s value (1.41 kg·m^{-1}·s^{-1}·kPa^{-1}), while lodgepole pine had the lowest (0.016 kg·m^{-1}·s^{-1}·kPa^{-1}) (Fig. 3). The species with higher K_s values in the spring generally also showed higher values in the summer, and the highest values were found for the deciduous species during both seasons (Fig. 3).

The interaction effect between species and time was not significant (P = 0.0965), which indicates that the effect of species on K_s was consistent across both spring and summer. However, K_s values differed significantly with respect to species (P = 0.0001) as well as time (P = 0.0001) (Fig. 3). Deciduous species varied significantly in their K_s values (P = 0.0001), and differed between spring and summer (P = 0.0106) (Fig. 3). However, within the evergreen group, K_s values did not vary significantly among species (P = 0.5485), but differed significantly between spring and summer (P = 0.0001) (Fig. 3). K_s values for the deciduous tamarack differed significantly from those for the deciduous broadleaf species (P = 0.0001), but did not differ from those for the other four coniferous species (P = 0.9335) (Fig. 3).

The K_s data for the 14 species were further analysed by pooling them into taxonomic groups, i.e., angiosperms and gymnosperms. Significant differences in K_s values were found between the two groups; angiosperms had higher K_s values than gymnosperms in both spring and summer (Fig. 4).

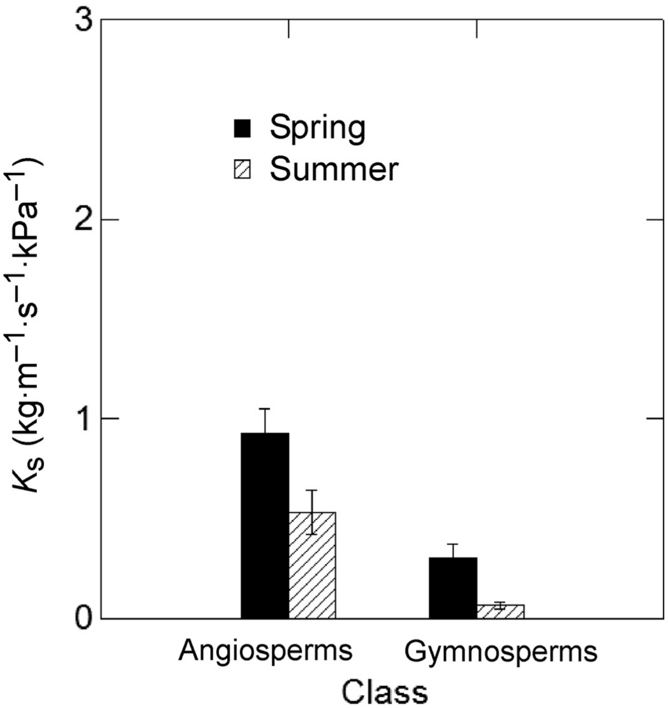
Discussion

HV measures a plant's sapwood investment on a leaf-area basis (Pallardy et al. 1995). A high HV implies that a large sapwood area is required to support a given amount of leaf area, while a low HV indicates a small sapwood investment per unit of leaf area. Leaf biomass was positively correlated with sapwood area of the branch base for Norway spruce, *Picea abies* (L.) Karst. (Dvorak et al. 1996), while O'Hara and Valappil (1995) found a significant relationship between leaf area and sapwood area for ponderosa pine. The relationship between the areas of tissues that conduct water and those that receive it is supposedly valid for conifers and angiosperms.

Vander Willigen and Pammenter (1998) found that HVs did not differ significantly among four *Eucalyptus* spp. clones, or between a mesic site and a xeric site. O'Hara and Valappil (1995) found that HVs were statistically similar for ponderosa pine growing in the overstory and understory. HVs did not differ significantly among the angiosperm species in this study, which agrees with Patiño et al.'s (1995) results. The values for conifers, however, differed significantly from each

© 2005 NRC Canada

Fig. 4. Specific hydraulic conductivity (K_s; mean ± 1 SE, n = 3) of angiosperm and gymnosperm species in sub-boreal forests in central British Columbia in the spring and summer.



other, and this finding agrees with Pallardy et al. (1995). The generally higher HVs for conifers means that they support fewer leaves on a sapwood-area basis than broadleaf species, and this could be a result of their reduced conductivity compared with angiosperms, or at least could mean that the low conductivities are somewhat compensated for by high HVs. The shade-intolerant interior Douglas-fir had the highest HV, which implies a low leaf area : sapwood area ratio, while the shade-tolerant subalpine fir had the lowest HV. The white spruce, *Picea glauca* × *englemannii* (Moench) Voss, a species very tolerant of shade, had a HV about half that of interior Douglas-fir. It should be noted that the very shade-intolerant tamarack had the lowest HV of the conifers, but this could be related to its deciduous habit rather than to its shade intolerance, i.e., more leaf area for a shorter photosynthesis season. HVs may thus be correlated with shade tolerance, and further studies could be devised to verify this across species.

The higher HVs for evergreen species may also be related to their late-successional status (Purves et al. 1998) compared with deciduous species. From a mechanical standpoint, a higher allocation of carbon to supporting tissues could theoretically be more advantageous for a long-lived species than for a short-lived one, although at the expense of photosynthetic tissues. Xylem efficiency in conducting water is important in relation to plant productivity (Spicer and Gartner 1998); however, the lower conductivities and higher HVs for conifers than for angiosperms may also be compensated for by the fact that most conifers are evergreen, and can thus transpire and photosynthesize for a much longer period than hardwoods (Pallardy et al. 1995). Also, Carey et al. (1998) found that allocation of carbon to woody tissues did not reduce tree growth in all instances for ponderosa pine growing at a xeric site compared with those at a montane site, which suggests that greater allocation to sapwood is not necessarily a disadvantage.

Hydraulic conductivity (K_h) is the most commonly measured parameter. Spicer and Gartner (1998) found that Douglas-fir branches of different ages did not differ in K_s or K_l values, while Ewers and Zimmermann (1984) found that K_s values were not statistically different in trunks and branches of similar diameters for balsam fir, *Abies balsamea* (L.) Mill. Vander Willigen and Pammenter (1998) found that K_s and K_l values did not differ significantly among four clones of *Eucalyptus* spp., and that K_s values were higher at a mesic site. Specific conductivity (K_s) is a measure of the porosity of the sapwood (Lemoine et al. 1999; Tognetti et al. 1999). A high K_s value implies efficient water conduction, whereas a low K_s value implies restricted flow. K_s has been positively correlated with vulnerability to xylem cavitation by freezing (Wang et al. 1992; Davis et al. 1999). K_s values have also been shown to differ significantly across species (Wang et al. 1992; Tognetti et al. 1999), and this was supported by finding from this study that the nine angiosperm and five gymnosperm species had very significantly different K_s values (Fig. 3). The angiosperms differed very significantly in K_s and K_l values, but the gymnosperms were found to have statistically similar K_s and K_l values (Patiño et al. 1995; Beck et al. 1999). This suggests that the sapwood of conifers, being composed of tracheids, which are a simpler, more uniform type of water-conducting cell (Pallardy et al. 1995), is similar in porosity across species, while angiosperm sapwood, which differs in anatomy (Wang et al. 1992), varies in porosity across species. The fact that K_s and K_l values for tamarack were significantly different from those for the angiosperms and not significantly different from those for the evergreen conifers suggests that K_s and K_l may not be related to leaf habit, although further study on other deciduous conifers, the broadleaf evergreen species, would be required to verify this proposition.

It is well established that K_s or K_l varies systematically with stem diameter in any given species, and that the relationship between the two is not the same for all species (Tyree and Zimmerman 2002). Consequently, differences seen between species at a particular diameter might not hold at other diameters. To eliminate this variation, a standard diameter (1.0 cm) was used in this study for all 14 species and the results were compared at the same time.

Tyree et al. (1998) proposed that rapid growth in pioneer species may be related to high K_s and K_l values. Fast-growing species that do not allocate much carbon to supporting tissues should, in theory, have a xylem that is more efficient at water conduction, so that the foliage is adequately supplied as a result of the high transpiration rates (Castro-Díez et al. 1998; Fort et al. 1998). Pioneer species such as paper birch, interior Douglas-fir, black cottonwood, *Populus trichocarpa* Torr. & Gray (Rood et al. 2000), willows, and Saskatoonberry had the highest K_s and K_l values in this study, thus supporting the above propositions. The results of this study also agree with those of Becker et al. (1999), who found significantly higher conductivity in colonizers than in late-succession species. However, this claim does not apply to some species, such as lodgepole pine in this study, which is

© 2005 NRC Canada

a pioneer species but has lower K_s and K_l values. The high K_l values found for these pioneer species imply that their leaves are well supplied with water, as K_l is essentially a measure of the hydraulic sufficiency of the sapwood.

It is known that angiosperms are more vulnerable than conifers to cavitation and embolism induced by winter freeze–thaw events (Wang et al. 1992; Davis et al. 1999). Drought-vulnerable populations of black cottonwood exhibited higher K_s values than drought-resistant ones (Sparks and Black 1999). Wang et al. (1992) also found that 43 north-temperate woody species with higher K_s values were more prone to lose conductivity by the end of the winter, while Tognetti et al. (1999) obtained the same result for 5 Mediterranean tree species. Conversely, Harvey and van den Driessche (1997) found K_s values to be higher in drought-resistant hybrid *Populus* clones, and Wakamiya-Noborio et al. (1999) found higher K_s values in pines from a drought-resistant population. The results obtained in our study agree with those of Becker et al. (1999) and Wang et al. (1992) in that higher K_s and K_l values were generally found for the pioneer species.

A higher incidence of winter embolism resulted in later bud burst in the spring for deciduous hardwoods, as was found by Wang et al. (1992). Deciduous species have a high demand for water in the spring at the time of bud flush (Castro-Díez 1998), and xylem that is efficient in water conduction may allow the increased transpiration rates required for high photosynthetic rates and fast growth at this time (Tognetti et al. 1999). Very significant differences in K_s values between the spring and summer sampling periods were found in this study (Fig. 3). The higher K_s values observed in the spring may be a physiological prerequisite for leaf flush at a time when water availability is high.

Acknowledgements

This research was supported by Forest Renewal British Columbia through project HQ96423-RE. Special thanks are extended to Tony Letchford and Antoine Lalumière for field sample collection and laboratory measurements. Comments from two anonymous reviewers improved the manuscript.

References

Becker, P., Tyree, M.T., and Tsuda, M. 1999. Hydraulic conductances of angiosperms versus conifers: similar transport sufficiency at the whole-plant level. Tree Physiol. **19**: 445–452.

Bond, W.J. 1989 The tortoise and the hare: ecology of angiosperm dominanace and gymnosperm persistence. Biol. J. Linn. Soc. **36**: 227–249.

Carey, E.V., Callaway, R.M., and DeLucia, E.H. 1998. Increased photosynthesis offsets costs of allocation to sapwood in an arid environment. Ecology, **79**: 2281–2291.

Castro-Díez, P., Puyravaud, J.P., Cornelissen, J.H.C., and Villar-Salvador, P. 1998. Stem anatomy and relative growth rate in seedlings of a wide range of woody plant species and types. Oceologia, **116**: 57–66.

Cruiziat, P., Cochard, H., and Améglio, T. 2002. Hydraulic architecture of trees: main concepts and results. Ann. For. Sci. **59**: 723–752.

Davis, S.D., Sperry, J.S., and Hacke, U.G. 1999. The relationship between xylem conduit diameter and cavitation caused by freezing. Am. J. Bot. **86**: 1367–1372.

DeLucia, E.H., Maherali, H., and Carey, E.V. 2000. Climate-driven changes in biomass allocation in pines. Global Change Biol. **6**: 587–593.

Dvorak, V., Oplustilova, M., and Janous, D. 1996. Relation between leaf biomass and annual ring sapwood of Norway spruce according to needle age-class. Can. J. For. Res. **26**: 1822–1827.

Enquist, B.J., and Niklas, K.J. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. Science (Washington, D.C.), **295**: 1517–1520.

Enquist, B.J., Brown, J.H., and West, G.B. 1998. Allometric scaling of plant energetic and population density. Nature (London), **395**: 163–165.

Ewers, F.W., and Zimmermann, M.H. 1984. The hydraulic architecture of balsam fir (*Abies balsamea*). Physiol. Plant. **60**: 453–458.

Fort, C., Muller, F., Label, P., Granier, A., and Dreyer, E. 1998. Stomatal conductance, growth and root signaling in *Betula pendula* seedlings subjected to partial soil drying. Tree Physiol. **18**: 769–776.

Harvey, H.P., and van den Driessche, R. 1997. Nutrition, xylem cavitation and drought resistance in hybrid poplar. Tree Physiol. **17**: 647–654.

Kavanagh, K.L., Bond, B.J., Aitken, S.N., Gartner, B.L., and Knowe, S. 1999. Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. Tree Physiol. **19**: 13–37.

Lemoine, D., Granier, A., and Cochard, H. 1999. Mechanism of freeze-induced embolism in *Fagus sylvatica* L. Trees, **13**: 206–210.

Maherali, H., and DeLucia, E.H. 2001. Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine. Oecologia, **129**: 481–491.

Mencuccini, M., and Grace, J. 1995. Climate influences the leaf area/sapwood area ratio in Scots pine. Tree Physiol. **15**: 1–10.

O'Hara, K.L., and Valappil, N.I. 1995. Sapwood – leaf area prediction equations for multi-aged ponderosa pine stands in western Montana and central Oregon. Can. J. For. Res. **25**: 1553–1557.

Pallardy, S.G., Èermák, J., Ewers, F.W., Kaufmann, M.R., Parker, W.C., and Sperry, J.S. 1995. Water transport dynamics in trees and stands. In Resource physiology of conifers: acquisition, allocation, and utilization. *Edited by* W.K. Smith and T.M. Hinckley. Academic Press, San Diego, Calif. pp. 301–389.

Patiño, S., Tyree, M.T., and Herre, E.A. 1995. Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to free-standing and hemi-epiphytic *Ficus* species from Panama. New Phytol. **129**: 125–134.

Purves, W.K., Orians, G.H., Heller, H.C., and Sadava, D. 1998. Life: the science of biology. 5th ed. Sinauer Associates, Sunderland, Mass.

Rood, S.B., Patino, S., Cooms, K., and Tyree, M.T. 2000. Branch sacrifice: cavitation associated drought adaptation of riparian cottonwoods. Trees, **14**: 248–257.

Sparks, J.P., and Black, R.A. 1999. Regulation of water loss in populations of *Populus trichocarpa*: the role of stomatal control in preventing xylem cavitation. Tree Physiol. **19**: 453–459.

Sperry, J.S., Donnelly, J.R., and Tyree, M.T. 1988. A method for measuring hydraulic conductivity and embolism in xylem. Plant Cell Environ. **11**: 35–40.

Spicer, R., and Gartner, B.L. 1998. Hydraulic properties of Douglas-fir (*Pseudotsuga menziesii*) branches and branch halves with reference to compression wood. Tree Physiol. **18**: 777–784.

Tognetti, R., Longobucco, A., and Raschi, A. 1999. Seasonal embolism and xylem vulnerability in deciduous and evergreen Mediterranean trees influenced by proximity to a carbon dioxide spring. Tree Physiol. **19**: 271–277.

© 2005 NRC Canada

Tyree, M.T. 2003. The ascent of water. Nature (London), **423**: 923–923.

Tyree, M.T., and Zimmermann, M.H. 2002. Xylem structure and ascent of sap. 2nd ed. Springer-Verlag, Berlin, Heidelberg, and New York.

Tyree, M.T., Patiño, S., and Becker, P. 1998. Vulnerability to drought-induced embolism of Bornean heath and dipterocarp forest trees. Tree Physiol. **18**: 583–588.

Vander Willigen, C., and Pammenter, N.W. 1998. Relationship between growth and xylem hydraulic characteristics of clones of *Eucalyptus* spp. at contrasting sites. Tree Physiol. **18**: 595–600.

Wakamiya-Noborio, I., Heilman, J.L., Newton, R.J., and Messina, M.G. 1999. Diurnal changes in water conduction in loblolly pine (*Pinus taeda*) and Virgina pine (*P. virginiana*) during soil dehydration. Tree Physiol. **19**: 575–581.

Wang, J., Ives, N.E., and Lechowicz, M.J. 1992. The relation of foliar phenology to xylem embolism in trees. Funct. Ecol. **6**: 469–475.

Waring, R.H., Schroeder, P.E., and Oren, R. 1982. Applications of the pipe model theory to predict canopy leaf area. Can. J. For. Res. **12**: 556–560.

Zhu, X.B., Cox, R.M., and Arp, P.A. 2000. Effects of xylem cavitation and freezing injury on dieback of yellow birch (*Betula alleghaniensis*) in relation to a simulated winter thaw. Tree Physiol. **20**: 541–547.

© 2005 NRC Canada