Annals of Forest Science (2012) 69:17–27
DOI 10.1007/s13595-011-0154-3

ORIGINAL PAPER

Effects of age-related increases in sapwood area, leaf area, and xylem conductivity on height-related hydraulic costs in two contrasting coniferous species

**Jean-Christophe Domec · Barbara Lachenbruch ·
Michele L. Pruyn · Rachel Spicer**

Received: 14 June 2011 / Accepted: 19 October 2011 / Published online: 16 November 2011

Abstract

• ***Introduction*** Knowledge of vertical variation in hydraulic parameters would improve our understanding of individual trunk functioning and likely have important implications for modeling water movement to the leaves. Specifically, understanding how foliage area (A_l), sapwood area (A_s), and hydraulic specific conductivity (k_s) vary with canopy position to affect leaf-specific conductivity (LSC) and whole-tree leaf-specific hydraulic conductance (K_l) may explain some of the contrasting patterns of A_l/A_s reported in the literature.

• ***Objective*** The general aim of the study was to characterize and compare the aboveground relationships between cumulative A_l, A_s, and k_s for two Pacific Northwest coniferous species with contrasting sapwood areas to give insight into size-related design of trees for water transport through changes in LSC and K_l.

• ***Results*** The 230-year-old ponderosa pine (*Pinus ponderosa*) trees had slightly smaller basal diameters than the 102-year-old Douglas-fir (*Pseudostuga menziesii*) trees, but contained 85% sapwood at the base compared to 30% in Douglas-fir. At the tree base, there was no evidence that A_l/A_s decreased with tree age or with tree size. In both species, A_l/A_s of branches was significantly higher than A_l/A_s at the tree base, but it was not different from A_l/A_s measured in the trunks at the top of the tree. Douglas-fir had higher A_l/A_s at the base than did ponderosa pine (0.42 vs. 0.24 m^2 cm^{-2}), similar patterns of change in A_l/A_s with height, and similar values of k_s, such that LSC in Douglas-fir was 77% the value of LSC in ponderosa pine. Compensating changes to increase LSC between short and tall trees occurred through an increased in k_s in tall trees but not through a reduction in A_l. LSC increased logarithmically with branch path length or trunk path length whereas K_l decreased significantly from top to base of old trees, but not between sections from old and young trees of similar cambial age.

• ***Conclusions*** Even though ponderosa pine had three times more sapwood than Douglas-fir, this study revealed a common relationship of declining K_l with increasing tree height and diameter between the two species, within age classes and among trees. There was no compensating decrease in A_l/A_s as trees got taller, which showed that a homeostasis in K_l was not maintained during growth. The

Handling Editor: Erwin Dreyer

Contribution of the co-authors J.-C.D. and B.L. designed research; J.-C.D., B.L., M.L.P. and R.S performed research; J.-C.D. analyzed data; and J.-C.D., B.L., R.S. and M.L.P wrote the paper.

J.-C. Domec
ENITAB, UMR 1220 TCEM,
33175 Gradignan, France

J.-C. Domec
INRA, UMR 1220 TCEM,
33883 Villenave d'Ornon, France

J.-C. Domec (✉)
Department of Forestry and Environmental Resources,
North Carolina State University,
Raleigh, NC 27795, USA
e-mail: jdomec@ncsu.edu

B. Lachenbruch
Department of Forest Ecosystems and Society,
Oregon State University,
Corvallis, OR 97331, USA

M. L. Pruyn
Department of Biological Sciences, Plymouth State University,
Plymouth, NH 03264, USA

R. Spicer
Department of Botany, Connecticut College,
New London, CT 06320, USA

trend of higher allocation of biomass to sapwood over leaves in ponderosa pine is consistent with this species' tendency to inhabit drier sites than Douglas-fir.

Keywords Tree conductance · Hydraulic limitation · Sapwood area/leaf area · Specific conductivity · Stand age

1 Introduction

The amount of water a tree can transpire depends, among other factors, on the balance between the potential water loss from the leaf surface area (A_l) (Oren et al. 1987) and the potential water flow through the conductive tissue or the sapwood cross-sectional area (A_s) (Simonin et al. 2007). Reports in the literature are mixed on the changes of A_l/A_s within and between trees of different ages or heights. For example some studies have found a constant ratio of A_l/A_s from the base to the top of the crown (Gould and Harrington 2008), whereas others have found a changing pattern (Dean and Long 1986; Gartner 2002). Comparing A_l/A_s values between trees of increasing height or age, some studies have demonstrated a decrease (McDowell et al. 2002a; Delzon et al. 2004), no change (Van Hees and Bartelink 1993), or an increase (Sellin 1987; Phillips et al. 2003).

The sapwood area is not a perfect estimate of the water flow that can pass through a location in a stem, however, because sapwood has different water transport capabilities in different locations. A rich literature on juvenile and mature wood in conifers has demonstrated that in typical stems, the wood at a tree tip and in a young plant (i.e., produced at locations where the cambium is young) have narrower shorter conduits than lower in the tree (Zobel and Sprague 1998). As a result, sapwood water permeability is lower in the tips and young plants than in the older parts of trees (Spicer and Gartner 2001; Rosner et al. 2006; Domec et al. 2008). The potential water flow through a given location on the stem is actually the product of the sapwood area times its water permeability that is defined by its specific hydraulic conductivity (k_s, kilograms per meter per second per megapascal):

$$k_s = Ql/A_s/\Delta P \tag{1}$$

where Q is the volume flow rate in kg s^{-1}, l the sample length (m) and ΔP represents the pressure difference between the two ends of the sample. Furthermore, the real capacity of the xylem at any one point to supply water to leaves is expressed not simply by A_l/A_s but by the leaf-specific conductivity (LSC):

$$\mathrm{LSC} = k_s A_s/A_l \tag{2}$$

Although it is expected that LSC be higher in trees growing in favorable environment (Sellin 2001), it can be seen from Eq. 2 that trees growing under conditions stimulating leaf area (such as fertilization or/and elevated CO_2 concentration) do not have necessarily lower values of LSC (Whitehead et al. 1984; Domec et al. 2010), because the adjustment in k_s does not always compensate for the increase in A_l/A_s (i.e., the decrease in A_s/A_l in Eq. 2). The variable LSC, however, is limited in that it does not take into account the resistance to water flow along the path and varies along the stem. Taking whole path length (H) into account, the water delivery per leaf area can be characterized by looking at the whole-tree leaf-specific hydraulic conductance (K_l):

$$K_l = \mathrm{LSC}/H \tag{3}$$

In contrast to the numerous reports on the effects of height on A_l/A_s, there are few studies on the effects of height on LSC and K_l. The length of the flow path from soil to leaf can vary substantially within trees, with potentially large differences in LSC and K_l between the top and bottom of the tree. Because there is good evidence that resistance in branches is much greater than in the stem (Sellin 2001; Domec et al. 2009; McCulloh et al. 2010), it is possible that branch A_l/A_s may be an equally important hydraulic adjustment to increased path length from the bottom to the top of the canopy (Mencuccini 2002). Most studies of hydraulic architecture showing a decline in LSC from trunks to branches and to leaves have been done on small trees, and very few data are available on large conifer trees with contrasting amounts of conducting tissue, or A_S. Understanding how A_l/A_s and k_s vary with canopy position to affect whole-tree LSC and K_l should improve mechanistic models of tree growth, and may explain some of the contrasting patterns of A_l/A_s reported in previous studies.

As trees get taller, the hydraulic path from root to tip becomes longer, and so it may be increasingly difficult to supply water to leaves at the tree top (Ryan and Yoder 1997; Phillips et al. 2002). Numerous studies using either transpiration and water potential to determine K_l or direct measures of k_s, A_s and A_l (Eq. 3) have shown that young trees have a higher K_l than old-growth trees despite large reductions in A_l/A_s (McDowell et al. 2002b; Delzon et al. 2004), and an increase in k_s with tree age (Domec and Gartner 2003; Rosner et al. 2008). Compensating changes between short and tall trees (as path length increases) would include any changes that limit the decrease in K_l and therefore permit plants to maintain high rates of transpiration. If size-related hydraulic limitation occurs, one could expect a reflection of this limitation in the functionally inter-related characteristics of A_l, A_s, and k_s (McDowell et al. 2002a, Tyree and Zimmermann 2002). Research has shown significant variation in wood k_s with radial position in the trunk, and in conifers a maximum usually occurs in the outermost rings and declines toward the heartwood/

sapwood boundary (Spicer and Gartner 2001; Domec et al. 2005). If patterns of k_s at different crown positions reflect the degree of cambial cell maturation (expressed as number of rings from pith) then young trees would behave the same as the same-aged tops of old trees if no adjustment in A_l/A_s occurs.

In the present study, we characterized A_l/A_s, k_s, LSC and K_l within and between two species from the Pacific Northwest with contrasting sapwood area and habitat. We studied Douglas-fir (*Pseudostuga menziesii* (Mirb.) Franco), a species with narrow sapwood (less than 8 cm) of about 20−40 rings in mature individuals, and ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws) that contrasts in having a wide sapwood (larger than 16 cm) made of 100−150 rings and living in drier environments. Studying species with wide and narrow sapwood allowed us to assess the generality of between- and within-trees relationships. We tested the following hypotheses: (1) trees increase basal k_s and decrease basal A_l/A_s as they get larger, such that K_l will decrease less than it would have had there been no adjustment to k_s and A_l/A_s. (2) Young trees have the same k_s and A_l/A_s and consequently the same LSC as the same-aged tops of old trees. (3) Branches have lower k_s and higher A_l/A_s than do trunks, but have the same K_l. (4) Species differ in K_l mainly through differences in A_l/A_s rather than differences in k_s.

2 Materials and methods

2.1 Sites and tree selection

We studied five age classes of Douglas-fir trees and four age classes of ponderosa pine trees (Table 1). Douglas-fir trees were classified as mature, intermediate, sapling, old seedling and young seedling. Ponderosa pine trees were classified as old-growth, mature, intermediate and sapling.

The mature Douglas-fir trees came from the Coast Range, Oregon, USA (42°57N, 123°21W), elevation 220 m, mean annual precipitation 1080 mm. After trees were felled, we marked the center of the internodes that were just distal to branch whorls at 5, 15, and 35 nodes from the tree top; at breast height, and at the tree's base (about 95 and 110 internodes from the top, respectively). The marked locations are hereafter referred to as being at the node, although they are actually just distal to (above) it. To avoid damaging branches upon harvesting, we also sampled three branches from each of these trees by climbing them before they were felled. Branches came from locations that were 5, 15, and 35 nodes from the top, and were sampled about 15 cm from the branch/stem junction. The intermediate Douglas-fir trees were harvested from each of two adjacent research plots on the H. J. Andrews Experimental Forest within the Willamette

Table 1 Stand characteristics (planted or natural regeneration) and mean (± s.e.) tree age and path length (trunk height or branch length), diameter at breast height (DBH), specific leaf area (SLA=A_l/leaf dry-weight), leaf area (A_l), leaf area to sapwood area at tree or branch base (A_l/A_s) and leaf-specific conductivity (LSC)

Age class	Tree part	Season	Stand origin	Age (year)	DBH (cm)	Path length (m)	*SLA* (cm^2 g^{-1})	Total A_l (m^2)	A_l/A_s (m^2 cm^{-2})	LSC (10^{-3} kg m^{-1} s^{-1}MPa)
Douglas-fir										
Mature	Bole	March	Nat. regen.	103±5	63.4±2.4	43.7±1.3	44.1±2.1	352±82	0.40±0.07	1.42±0.26
Mature	Bole	Sept.	Nat. regen.	100±2	60.7+1.6	43.6+1.1	63.0±3.2	309±41	0.44+0.06	1.45±0.16
Intermediate	Bole	Sept.	Planted unthinned	34±2	21.6±0.6	22.1±0.6	77.4±2.9	49.5±7.3	0.32±0.03	1.44±0.20
Intermediate	Bole	Sept.	Planted thinned	34±2	24.6±1.2	20.1±0.9	69.3±4.5	94.5±18.3	0.38±0.05	1.07±0.12
Sapling	Bole	Sept.	Nat. regen.	10.0±0.3	7.0±0.7	5.7±1.8	98.0±2.9	17.3±3.3	0.35±0.03	0.97±0.08
Old seedling	Bole	Sept.	Planted	5	3.3±0.2	1.7±0.1	76.7±0.7	1.6±1.3	0.23±0.04	0.33±0.03
Young seedling	Bole	Sept.	Planted	3	1.0±0.2	0.9±0.1	86.6±2.9	0.16	0.18±0.04	NA
Mature	Branch	Sept.	Nat. regen.	5	1.2±0.4	0.5±0.1	41.8±0.5	0.62±0.09	0.60±0.11	0.18±0.05
Intermediate	Branch	Sept.	Nat. regen.	5	1.0±0.1	0.6±0.1	91.4±4.9	0.34±0.07	0.51±0.05	0.16±0.01
Ponderosa pine										
Old-Growth	Bole	March	Nat. regen.	222±27	62.3±1.9	33.3±0.4	67.7±1.6	540.4±34.7	0.23±0.02	1.99±0.06
Old-Growth	Bole	Sept.	Nat. regen.	243±10	71.9±1.7	34.3±0.4	71.0±0.9	745.6±72.4	0.26±0.02	1.79±0.18
Mature	Bole	Sept	Nat. regen.	72±5	25.9±2.2	12.4±0.9	69.5±1.8	76.7±15.9	0.21±0.01	1.34±0.15
Intermediate	Bole	Sept.	Nat. regen.	40±5	13.2±0.6	5.8±0.5	76.6±1.0	23.6±5.2	0.19±0.02	0.58±0.06
Sapling	Bole	Sept.	Nat. regen.	21±5	9.4±0.5	3.3±0.2	77.0±1.9	18.9±6.9	0.20±0.03	0.48±0.05
Old-Growth	Branch	Sept.	Nat. regen.	5	0.7±0.4	0.4±0.1	50.1±0.9	0.16±0.03	0.40±0.03	0.35±0.05
Intermediate	Branch	Sept.	Nat. regen.	5	0.8±0.2	0.5±0.1	52.9±0.9	0.18±0.02	0.35±0.02	0.36±0.04
Sapling	Branch	Sept.	Nat. regen.	5	0.7±0.1	0.4±0.1	55.0±0.9	0.17±0.01	0.46±0.02	0.27±0.03

National forest (44°15N, 122°10W), elevation 705 m, mean annual precipitation 2300 mm. The trees were planted in 1963 following clear-cutting, then thinned in 1981 from about 3,460 to 600 trees/ha or left untreated. In July 1995 and in June 1997, six trees were harvested from the unthinned stand and six trees were harvested from the thinned stand. After felling the trees, we marked the center of each internode 5, 10, 15, and 20 nodes from the tree top, and also marked breast height, and the tree's base (about 25 and 30 internodes from the top, respectively). Studying trees from thinned and unthinned stands allowed us to test how strong the relationships between A_l, A_s, and k_s hold for a wider range of growing conditions. Douglas-fir saplings came from the same site as the mature trees. Six 10-year-old saplings were harvested in March 1999. They were sampled five nodes down for the top and at the base. Lastly, 5- and 3-year-old Douglas-fir seedlings were grown in outdoor nursery beds in Corvallis, OR (44°39′ N, 123°14′ W, 130 m elevation) and randomly selected 24 in March 2000 for study. All seedlings were sampled at their bases only.

All ponderosa pine trees came from a mixed-age stand located on the eastern side of the Oregon Cascade Range (43º32′N; 121º41W) on a private forestland (Crown Pacific Co.) at elevation 1,355 m and with mean annual precipitation of 645 mm. The stand is a mix of ponderosa pine and lodgepole pine (*Pinus contorta*) ranging from 15 to 400 years old, and with approximately 250 trees/ha. Six old-growth trees (>220 years old) in March 1999, and six others in September 1999 were selected based on their cambial age at breast height (estimated from increment cores), their height as a rough indication of age cohort and their health (free of broken tops, stem deformities or disease). Six mature trees (>70 years old) in March 2000, and five intermediate (>40 years old) and six young trees (>20 years old) in September 2000 (Table 1) were also selected. The old-growth and mature trees sampled were the same trees studied by Pruyn et al. (2003), Domec and Gartner (2003) and Domec et al. (2005). The target internodes for old-growth trees was nodes 15, 50, the bole section two-thirds of the way between the top and the base of the live crown (called crown base), and the tree base. Mature trees were sampled at nodes 15, 50, and the base. The intermediate and young trees were sampled at node 15 and the base,

2.2 Leaf areas

Total tree leaf area above each sampled node was determined as described by Domec and Pruyn (2008). Briefly, foliage attached to and distal to each segment was collected to determine leaf dry mass, and subsampled to determine fresh area/dry mass conversions. We divided each tree into one (saplings), two (seedlings), three (intermediate) or four (mature and old-growth trees) vertical sections. We subsampled each section as follows. For the old-growth and mature trees, we determined fresh weight for 25% of the mass (the foliage plus the attached woody material) in each of the lower zones, and 100% of the mass for the top zone. We recorded the fresh mass of the clipped material using spring scales in the field. A subsample of the clipped material was then saved for each zone to determine the conversion from needle fresh weight to needle dry weight. We dried the subsamples, separated leaves from woody twigs and branches and recorded their dry mass. For each segment and foliar class, 20 fresh needle fascicles were removed from five randomly selected sprigs. The remaining foliage was dried in an oven for 48 h at 60°C and weighed. For Douglas-fir needles, the projected area of fresh foliage samples was determined using a video camera and NIH Image version 1.52 (public domain software). Because ponderosa pine has three-needled fascicles with stomata on all surfaces, all leaf area data were expressed on an all-sided leaf area basis. The projected area of each ponderosa pine needle was measured using a digital caliper, and assuming that all three needles of each fascicle represents a cylinder, the conversion factor 2.36 was used to determined the all-sided leaf area. The samples were then dried and weighed to establish the specific leaf area (SLA) corresponding to fresh area to dry mass ratios. Conversion ratios between total tree fresh mass, subsample fresh mass, and subsample dry mass were used to calculate the fresh leaf area distal to each segment for use in calculations of leaf-based conductivities (see below). For the saplings, intermediate and younger trees we saved 100% of the mass in all zones, but processed the samples identically to the old trees.

2.3 Sapwood samples and specific conductivity (k_s)

After trees were felled, we measured total tree height and removed replicate disks from the target internodes. The disk for measuring k_s was wrapped in dark plastic for transportation and stored under water until measurements were undertaken. The second disk was used to estimate xylem width, sapwood area, heartwood area and proportion of sapwood (Table 2).

Within the Douglas-fir trees, two samples for k_s were outlined in pencil on the cross-section of each disk, one sample from the innermost sapwood (adjacent to, but not including, the heartwood/sapwood boundary), and one from the outermost sapwood (adjacent to, but not including, the cambium and current year's growth ring). For the breast height disk only, a third sample was drawn midway between the inner and outer sapwood positions. For the ponderosa pine trees, because of the wide sapwood, two more samples were outlined at equal distance between the outer and inner samples. All samples had roughly similar cross-sectional area, resulting in a variable number of rings per sample, from three to seven, depending on position in the tree. Compression wood, traumatic resin canals and

Table 2 Xylem and sapwood characteristics at the bases of trees ranging from 103 (mature) to 5 years old (seedlings) for *Pseudotsuga menziesii* trees and from 235 (old-growth) to 20 years old (young) for *Pinus ponderosa* trees (mean±s.e.)

Species	Age class	Total xylem area (cm^2)	Sapwood width (cm)	Sapwood area (cm^2)	Proportion of sapwood (%)	Number of sapwood rings	Inner sapwood k_s relative to outer sapwood k_s
Douglas-fir							
	Mature	2650±120	7.2±0.7	759.6±80.6	30±5	30±2	1.18±0.06
	Intermediate	331±24	3.8±0.3	200.5±17	53±3	10±2	0.75±0.05
	Young	55±4	1.9±0.2	47.8±1.8	89±4	9±2	0.46±0.08
	Seedlings	7±1	0.6±0.1	6.9±0.7	99±2	4	N/A
Ponderosa pine							
	Old-growth	2950±162	17.9±1.6	2506±137	85±3	122±8	0.80±0.07
	Mature	389±71	9.8±0.7	374.9±71.1	97±1	54±3	0.51±0.05
	Intermediate	126±25	6.30±0.56	122.1±12.9	98±2	39±6	0.59±0.07
	Young	90±12	5.29±0.23	89.7±30.1	99±1	19±1	N/A

knots as well as light-colored rings adjacent to the heartwood were avoided. Samples were first sawn from disks with a small band-saw, and then radial and tangential surfaces were elaborated with chisels while keeping the sample wet. About 2 cm were sawn off each axial end leaving a sample about 15 cm long. The cross-sectional ends were then surfaced with a razor blade and samples were stored in water until measured. Final samples were 90−110 mm long, with cross-sections ranging from 170 to 190 mm^2.

Specific conductivity (k_s, kilograms per meter per second per megapascal) was calculated according to Darcy's law (Eq. 1). We measured k_s using a membrane-lined pressure sleeve to prevent fluid from leaking from the sides of samples (Spicer and Gartner 1998). One end of the pressure sleeve was attached by tubing to a reservoir filled with filtered (0.22 µm) water adjusted with HCl to pH 2 that delivered a pressure head of 5.2 kPa. A 1-ml graduated pipette was attached to the other end and volume flow rate was measured by timing the movement of the meniscus across 0.1 ml graduations. The temperature of the solution was recorded and all calculations of k_s were corrected to 20°C to account for changes in fluid viscosity with temperature. Following k_s measurements, whole segments were perfused with filtered (0.22 µm) 0.5% safranin-O for 20 min. The earlywood always stained completely, giving no evidence of embolism.

2.4 Leaf-specific conductivity and leaf-specific conductance (K_l)

The efficiency of xylem in conducting water was expressed by the leaf-specific conductivity (LSC, kg m^{-1} s^{-1} MPa^{-1}), which at a given node in the trunk or at the base of a branch is k_s divided by A_l/A_s of the given segment (Eq. 2). Leaf-specific hydraulic conductance (K_l, kg m^{-2} s^{-1} MPa^{-1}) is defined as the ability of wood at a given node to supply water to leaf, per meter of stem or branches and was computed by dividing LSC by the height or the branch length (H, m) considered (Eq. 3).

2.5 Statistical analysis

Least squares methods were used to fit relationships between A_l/A_s, k_s, LSC, K_l and tree height, stem diameter or cambial age. All stated equations in the figures had a significant regression coefficient at $P<0.05$. Differences between old and young trees and among locations were determined using a one-way ANOVA. The experiment was designed to assess values of k_s at several sapwood depths, but for height position we were interested in an estimate of the entire sapwood. Therefore, the effect of height position was estimated by weighting the values by the proportion of the total sapwood area occupied by each sapwood depths. All statistical procedures were conducted with Statistical Analysis Systems software (SAS Inc., Cary, NC, USA).

3 Results

3.1 A_l/A_s and tree size or age

At the bases of the trees, the old ponderosa pines had slightly smaller diameter (Table 1) but significantly more sapwood ($P=0.001$) than the old Douglas-firs (Table 2). Sapwood proportion increased significantly with age in Douglas-fir ($P=0.02$) but did not vary in ponderosa pine ($P=0.19$). The values for sapwood proportion were the same at the base of Douglas-fir as at 1 m, although the absolute area of the xylem was 12% higher at the base than at 1 m.

Among the four age classes of ponderosa pine, SLA (A_l/leaf dry-weight) was not significantly different ($P>0.28$), whereas in Douglas-fir trees it was approximately 50% higher ($P=0.02$) in young trees (seedlings and saplings) than in mature trees (Table 1). For both species, there was an increase in SLA from March to September ($P<0.03$). In ponderosa pine, A_l was 38% higher in September than in March ($P=0.01$) because trees had two cohorts of foliage. In Douglas-fir that carries up to 5 years of needles there was no difference in A_l between March and September ($P=0.56$).

Leaf area/sapwood area (measured as cumulative leaf area/ sapwood area at the base of the tree, $A_{\text{l-base}}/A_{\text{s-base}}$) increased in both species ($P<0.01$) from seedlings to mature and old-growth trees (Fig. 1). The $A_{\text{l-base}}/A_{\text{s-base}}$ was about twice as high in Douglas-fir as in ponderosa pine (Table 1). Within both species, there were positive correlations between tree height and $A_{\text{l-base}}/A_{\text{s-base}}$ (Fig. 1a) and between cambial age and $A_{\text{l-base}}/A_{\text{s-base}}$ (Fig. 1b). The slope of the increase of $A_{\text{l-base}}/A_{\text{s-base}}$ with tree height or tree age, however, was more than twice as high in Douglas-fir than in ponderosa pine. Also, because of the difference in stomatal arrangement, the estimated A_l in ponderosa pine was calculated on the basis of the entire leaf surface area (2.36 times the projected area, see Methods), but in Douglas-fir it was on the basis of one-sided area. Therefore, these numbers cannot be used directly to compare biomass allocation patterns but rather leaf water loss.

3.2 A_l/A_s relative to position within tree

To test whether young trees have the same A_l/A_s as the same-aged tops of old trees, we also looked at values for the top 15 nodes of a tree, regardless of tree age and height. In the trunk, the value $A_{\text{l-node 15}}/A_{\text{s-node 15}}$ was higher in old/tall trees than young/short trees and followed the same pattern for both species (Fig. 2). At the branch level, $A_{\text{l-branch}}/A_{\text{s-branch}}$ in Douglas-fir varied significantly with canopy height, with branches at node 35 exhibiting a significantly lower $A_{\text{l-branch}}/A_{\text{s-branch}}$ than branches at node 5 and 15 (0.27 versus 0.55 $m^2\ cm^{-2}$; $P=0.03$). In both species, $A_{\text{l-branch}}/A_{\text{s-branch}}$ was significantly higher ($P<0.03$) than trunk $A_l/A_{\text{s-base}}$ (Table 1, Fig. 1), but was not significantly different ($P>0.27$) than trunk $A_l/A_{\text{s-top}}$ (Table 1, Fig. 2).

The A_l/A_s was low at the base of the tree (on the right side of graph, Fig. 3a), increased gradually upward within the tree, and then decreased in the upper 10−15 nodes in both old and young Douglas-fir trees (Fig. 3a). The young thinned Douglas-fir stand exhibited a 19% increase in A_l/A_s over the unthinned stand ($P<0.01$). The same increased in A_l/A_s existed from the bottom to the top of old and mature ponderosa pine, except that A_l/A_s did not decline at the tip (Fig. 4a). In both species A_l/A_s was significantly higher in September than in March ($P<0.04$; Table 1; Fig. 3a and 4a).

3.3 k_s and LSC within trees

For both species, k_s was lowest ($P<0.01$) in branches than in any trunk locations. Branch k_s was significantly higher ($P=0.03$) in Douglas-fir where it ranged from 0.62 to 0.87 kg $m^{-1}\ s^{-1}$MPa than in ponderosa pine where it ranged from 0.25 to 0.35 kg $m^{-1}\ s^{-1}$MPa. The values of trunk k_s were similar for the two species and the two age groups shown in Figs 3b and 4b. For both species, k_s was lowest at the tip of the tree (low cambial age), rose in the mid-section of the bole, and then declined to an intermediate value at the tree base (high cambial age) (Fig. 3b for old and young Douglas-fir, and Fig. 4b for old and mature ponderosa pine). For both species in the upper positions in the old trees, k_s of the inner sapwood was 38–47% lower ($P=0.02$) than k_s of the outer sapwood. In contrast, at the base of the Douglas-fir trees, inner sapwood had higher k_s than outer sapwood (Table 2).

The value of LSC increased rapidly at the base of both age classes of Douglas-fir and then declined throughout the upper part of the stem to the tip, with the steepest slope near the tip, and falling to a value lower than at the base (Fig. 3c). In Douglas-fir, there was not seasonal effect on LSC because the increase in A_l/A_s between March and September was compensated by an increase in k_s. Old and mature ponderosa pine trees had a similar pattern, but without the initial rise at the base: values were high at the base and declined toward the tip (Fig. 4c). In ponderosa pine, the seasonal increase in k_s between March and September was not enough to compensate for the increase in $A_l/A_{s,}$ and thus LSC was significantly higher in March than in September ($P<0.001$). The seasonal increases in k_s between March and September were probably because the new outer sapwood ring formed during the growing season became hydroactive (Figs 3b, 4b).

3.4 k_s, LSC and K_l between and within trees

Although ponderosa pine k_s values were significantly higher ($P=0.02$) between 50–100 years old, both species appeared to fall on the same asymptotic curve for k_s vs. cambial age (Fig. 5), rising from low cambial age and then leveling off around 30 years. The fitted species-specific asymptotic curves of k_s as a function of cambial age were not different ($P=0.27$).

At the base of the tree, LSC was significantly lower ($P<0.02$) for the youngest stands studied than for the older stands of either species (Table 1). LSC increased linearly (Fig. 6a) and K_l decreased logarithmically (Fig. 6b) with axis diameter. In both species, LSC of large diameters (40–60 cm) stems was 8 times larger than that of small diameter (1 cm) branches. Both stem or branch fell on the same line indicating that values of LSC and K_l of young trees were similar to those of the top of the old trees for a given diameter (Fig. 6a, b). By excluding the branch samples, the slopes of the relationships between of LSC and K_l as a function of axis diameter were not significantly different ($P=0.21$ and $P=0.41$ for LSC and K_l, respectively).

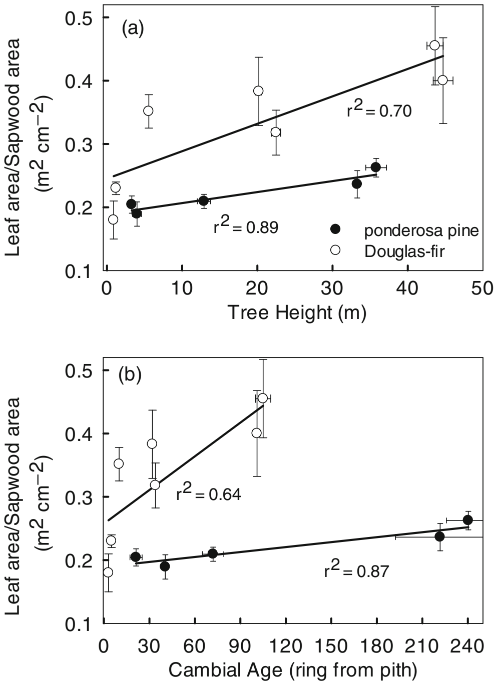

Fig. 1 **a** Effect of height and **b** effect of tree age on $A_l/A_{\text{s-base}}$ for Douglas-fir and ponderosa pine trees from different aged stands. Each point represents a set of trees with different heights or ages and not different heights or ages within one tree. Values show mean±s.e. (n=5 to 24)

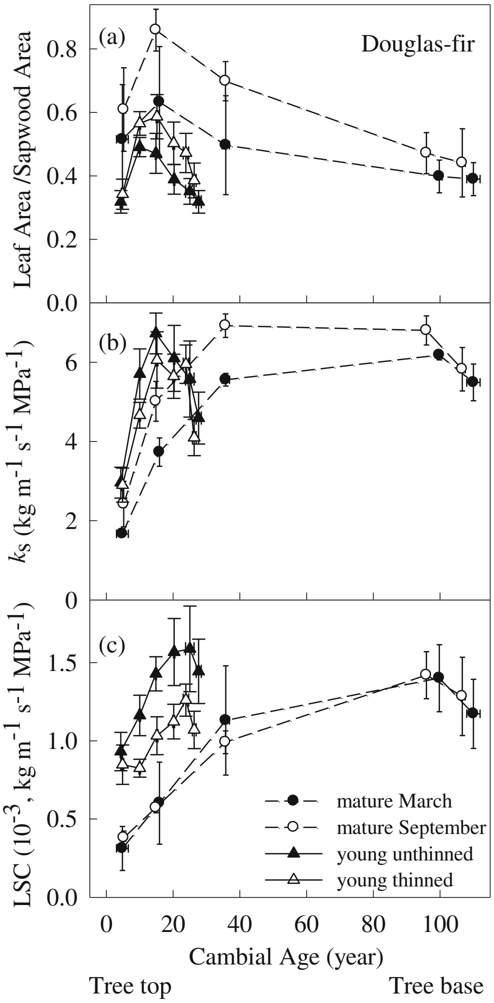

Fig. 3 **a** Leaf area/sapwood area (in per square meter per centimeter) and **b** specific conductivity (k_s) and **c** leaf-specific conductivity (LSC) by vertical position in the tree for mature and young Douglas-fir trees (each point shows mean±s.e. for n=5–6 samples). The March harvest was before current year's growth had started, and the September harvest was near the end of current year's growth. The two young stands were adjacent to one another

Values of LSC and K_l of young trees were the same as those of top of the old trees for a given cambial age (Fig. 7a, b). LSC was lower at the top of the tree than at the bottom, leveling off at 0.018±0.001 and 0.015±0.001 kg m^{-1} $s^{-1}MPa^{-1}$ for Douglas-fir and ponderosa pine respectively (Table 1, Fig. 7a). Maximum LSC at the tree base in old trees was about 1.3 times higher in ponderosa pine than Douglas-fir. In other words, old Douglas-fir supports almost 1.3 times the leaf area as old ponderosa pine per unit conductive capacity of the sapwood. However, for branches or tree heights ranging from 0 to 10 m, the values of LSC were similar for both species (Fig. 7a). The trends in K_l with tree height or branch length did not differ significantly within and between species (Fig. 7b).

LSC increased logarithmically with branch path length or trunk path length (Fig. 7a) whereas K_l decreased logarithmically with path length (Fig. 7b). Branches had a K_l twice as high as young trees and more than four times as high as old trees. The increase in LSC with tree height limited the expected reduction in K_l by more than 50%. Assuming a constant LSC, the drop in K_l with tree height was faster for young and intermediate trees, or trees between 5 and 20 m in height, than for old trees (see dashed the line compared to the fitted line in Fig. 7b).

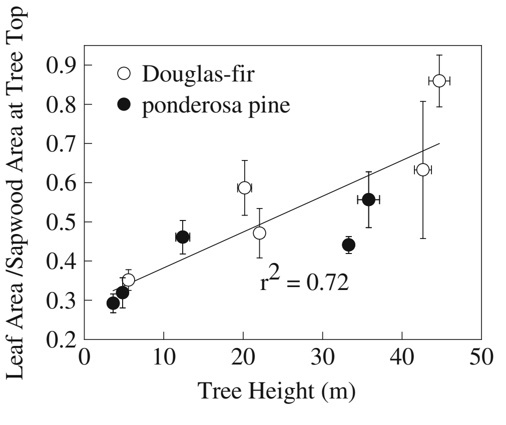

Fig. 2 Leaf area/sapwood area (in m^{-2} cm^{-2}) at node 15 from tree top versus tree height for Douglas-fir and ponderosa pine trees (each point shows mean±s.e. for n=5–6 samples)

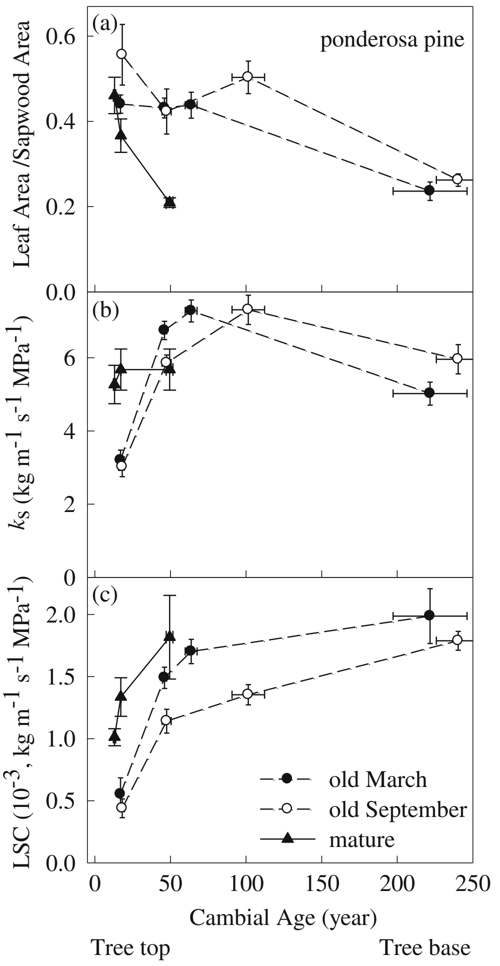

Fig. 4 **a** Leaf area/sapwood area (in per square meter per centimeter) and **b** specific conductivity (k_s) and **c** leaf-specific conductivity (LSC) by vertical position in the tree for old-growth and mature ponderosa pine (each point shows mean±s.e. for $n=6$ samples). The March harvest was before current year's growth had started, and the September harvest was near the end of current year's growth

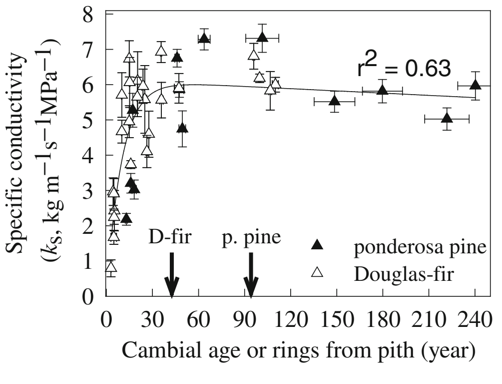

Fig. 5 Effect of cambial age on specific conductivity for Douglas-fir and ponderosa pine trees from different aged stands. The *arrows* represent the base of the live crown for mature Douglas-fir (*D-fir*) and old-growth ponderosa pine (*p. pine*). Values show mean±s.e. ($n=5$ to 24)

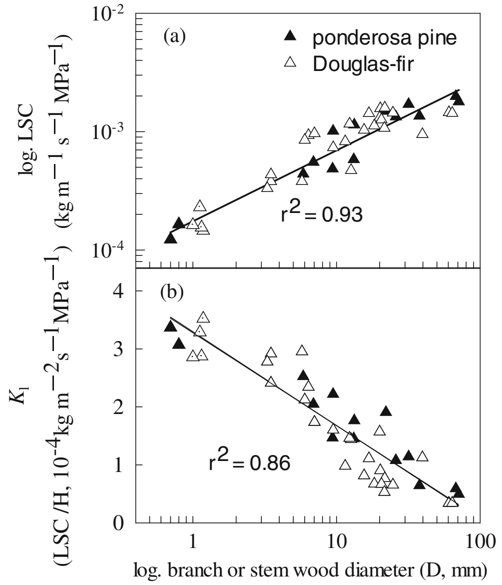

Fig. 6 **a** Effect of section diameter (on a log. base 10 scale) on leaf-specific conductivity (LSC) and **b** leaf hydraulic conductance (K_l) for Douglas-fir and ponderosa pine trees from different aged stands. Each point represents the mean values for each height in the trees and at the base (whole tree). *Dotted triangles* represent branch samples. The lines in **a** and **b** were defined by the following equations: LSC=1.7×10^{-4} $D^{0.6}$, and K_l=0.7ln$D$+3.3, respectively, where D is the organ (stem or branch) diameter in cm

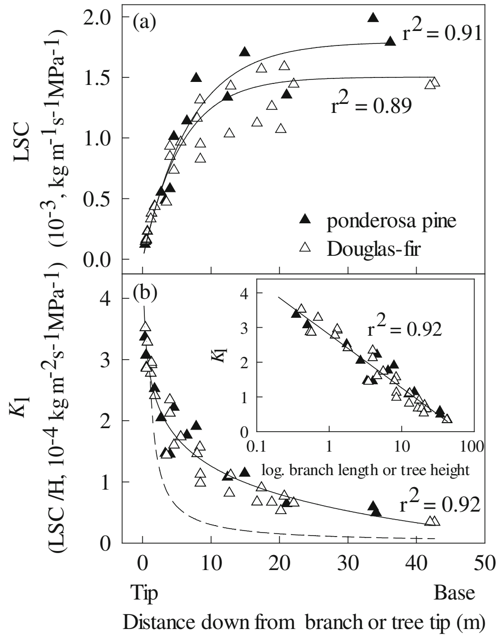

Fig. 7 **a** Effect of section height (distance down from branch or tree) on leaf-specific conductivity (LSC) and **b** leaf hydraulic conductance (K_l) for Douglas-fir and ponderosa pine trees from different aged stands. Each point represents the mean values for each height in the trees and at the base (whole tree). Logarithmic functions provided the best fit. The *dashed line* represents the fit from an inverse relationship between tree height and K_l assuming no increase in LSC with tree age when using the youngest sample of a species as starting point. The insert represents K_l versus the log. base 10 of section height

4 Discussion

Our results supported the hypothesis that as trees get taller, the hydraulic path length from root limits the supply water to the leaves (Ryan and Yoder 1997; Phillips et al. 2002). As stated in the introduction, if hydraulic limitation limits tree size then some functional A_l, A_s and k_s should be affected. The first hypothesis was that trees increase basal k_s and decrease basal A_l/A_s as they get larger, such that K_l will decrease less than it would have had there been no adjustment to k_s and A_l/A_s (see dashed line in Fig. 7b). Our study party supported this hypothesis. From a vascular perspective, the base of the old-growth trees appeared to be almost three times more efficient in supplying water than the base of the young trees as shown by k_s and by LSC. However, this vascular advantage did not compensate for tree size. Low K_l in old trees was supported by increasing k_s (Whitehead et al. 1984) but was compounded by increasing A_l/A_s (Phillips et al. 2003) and the increase of LSC was possible in old trees because the increase in k_s was higher than the increase in A_l/A_s.

From an ecological point of view, a reduction in A_l/A_s in ponderosa pine trees induced higher LSC, which has implications for this species' adaptation to dry habitats (Simonin et al. 2007). Higher LSC in ponderosa pine meant that those trees required a smaller drop in trunk xylem pressure potential to draw the same amount of water to the leaves, thereby maintaining xylem water potential at values less likely to cause embolism (Dalla-Salda et al. 2011). This agreed with the vulnerability curves between Douglas-fir and ponderosa pine (Domec et al. 2009). High allocation of biomass to sapwood and a resulting decrease in basal A_l/A_s may also be treated as a compensation for low k_s in young trees growing under a low light regime or under shade of taller trees (Renninger et al. 2007). Young and short trees were not yet producing mature wood, which explains the low k_s found in young trees (Fig. 5; Spicer and Gartner 2001; Domec and Gartner 2002). Low k_s due to cambium maturation also explained why there was a step decrease in LSC within the crown in both species. Young trees also invested more leaf area per leaf dry weight (SLA) than mature trees (Table 1), which may reflect an optimization of photosynthetic rate at the individual plant level (Greenwood et al. 2008). The differences in the SLA patterns between young and old trees also reflected that Douglas-fir is an intermediate shade-tolerant species, while ponderosa pine is shade-intolerant.

The second hypothesis was that young trees have the same k_s and A_l/A_s as the same-aged tops of old trees. This hypothesis was not totally supported across the three different age classes because A_l/A_s at tree top increased with tree age. On the other hand, the occurrence of similar LSC and K_l between young trees and the same-aged tops of old trees appeared to be the case. The similarities in K_l signify that the water potential difference needed for a constant transpiration rate, will be the same within young trees and between the lower part of the crown to the top of old trees. Low A_l/A_s in young trees and at the top of old trees as compared to A_l/A_s at tree base could perhaps be the primary mechanism that permits increases in LSC and transpiration without changes in water potential (Gonzalez-Benecke et al. 2011). Young trees, for example, must buffer environmental conditions because of a shallow rooting depth and the top of a tree must compete for water with lower regions in the trunk. Between trees, high A_l/A_s in mature trees could also reflect a mechanism to enhance LSC at the shoot level. Since the majority of the branch hydraulic resistance is located in the leaves, a larger A_l/A_s can potentially increase the total leaf hydraulic conductance because of the presence of a greater number of needles connected in parallel relative to sapwood. Our result also showed that within trees, A_l/A_s was higher in branches than in the stems.

The third hypothesis was that branches have lower k_s and higher A_l/A_s than do trunks, but have the same K_l. The strong relationship between k_s and cambial age across species and between LSC and stem/branch diameter stresses the idea that a functional convergence exits among woody plants (Tyree and Zimmermann 2002; Meinzer et al. 2008). Although ponderosa pine had a higher rate of water flow per unit A_l as shown with the LSC values, both species showed a pronounced trend of an exponential rise in LSC with increasing stem diameter within a tree proximally from branches to the trunk (Ewers and Zimmermann 1984; Tyree et al. 1984). In order to increase hydraulic efficiency per unit carbon investment, water transport in conifers appears to require wide conduits at the base feeding smaller diameter conduits at the top (McCulloh and Sperry 2005; McCulloh et al. 2010). However, as a consequence of this the optimum network, wide diameter conduits at the base of tall trees increase transport efficiency when the tree has little drought stress but increase vulnerability to embolism when the plant is operating in dry conditions (which is most likely the reason why k_s does not keep increasing with cambial age, Fig. 5). Trunks of mature and old-growth trees have lower safety factors toward embolism than have tree tops and branches in these two species (Domec et al. 2009). This trend of needing wider conduits at the base also explains why as trees get taller, their calculated K_l will converge on the predicted K_l (Fig. 7b). In old trees, the increase in A_l/A_s associated with a slowing down or even a decline in k_s will be such that eventually K_l will reach values close to zero. When the plot of gradient of K_l versus height was extrapolated to K_l=0 (Fig. 7b, inset), the estimated values of tree height was close to 70 m, close to the average maximum heights encountered by these species on those sites.

The fourth hypothesis was that species differ in K_l through differences mainly in A_l/A_s rather than differences in k_s. Contrary to our fourth hypothesis, and even though ponderosa pine had three times more sapwood than Douglas-fir, this study revealed a common relationship of declining K_l with increasing tree height and diameter between the two species, within age classes and among trees (Figs 6, 7). In general, there is a strong relation between the diffusive conductance of stomata to water vapor (g_s) and the aboveground efficiency of the plant water transport system (Meinzer et al. 2008; Domec et al. 2010), which may be part of the reason for the decline in forest productivity with age (Ryan et al. 2007; Greenwood et al. 2008). By combining Darcy's law and the Penman–Monteith equation, Whitehead et al. (1984) described whole tree aboveground hydraulic adjustments of conifers in response to increased transpiration demands:

$$g_s = A_s/A_l k_s(\Delta\Psi/H)c/D \quad or \quad g_s = K_l \Delta\Psi c/D \tag{4}$$

where $\Delta\Psi/H$ is water potential gradient, D is time-averaged vapor pressure deficit of the air, and c is a coefficient representing air and water thermodynamic properties. Under the same evaporative demand, Eq. 4 predicts that within a species, if K_l decreases with increasing height and age, so should g_s unless $\Delta\Psi$ can overcompensate the drop in K_l (Schäfer et al. 2000). However, previous research shows that the low K_l in the old trees is not supported by the development of a large water potential difference from the soil to the shoot, so g_s should decline and increasingly limit photosynthetic assimilation in older trees. On different trees growing in the same sites, it has been shown that the difference in trunk xylem driving force was around 1.55 MPa in Douglas-fir trees (Domec and Gartner 2002) and 1.50 MPa in ponderosa pine trees (Irvine et al. 2004; Domec et al. 2005). For old trees to maintain the same g_s as young trees, their water potential gradient should be around 5.5 MPa, which would put extremely large stresses on the conducting system and would induce more than 85% embolism (Domec and Gartner 2002; 2003; Dalla-Salda et al. 2011; Gonzalez-Benecke et al. 2011). Furthermore, the model (Eq. 4) also predicts that because K_l increases from the bottom to the top of the crown (as shown in Fig. 7b), g_s should also vary within tree (Schäfer et al. 2000).

We conclude that even though there was an increase in LSC with increasing tree height and with diameter, we found no compensating decrease in A_l/A_s as trees got taller, which showed that a homeostasis in K_l was not maintained during growth. The A_l/A_s relationship was not simply mediated by k_s. Ponderosa pine achieved high values of LSC by having wide sapwood and small leaf area, but assuming the two factors are co-evolved, we do not know which factor constrained the other. Knowledge of vertical hydraulic parameters would not only improve the understanding of individual trunk functioning such as the role played by xylem k_s in determining patterns in sap flux density (James et al. 2003; Domec et al. 2006), but would also have important implications for modeling water movement to the leaves and assessing the significance of tree age for hydraulic performance (Williams et al. 2001; Phillips et al. 2002). Many models have been proposed to describe water movement within trees and to predict tree transpiration with varying degrees of success (Williams et al. 2001; Ogée et al. 2003). Our study provides empirical data that can be for example be used in such theoretical hydrodynamic models to track midday water potentials in the different parts of the tree system and see which of these water potentials is more effective in affecting g_s.

Acknowledgments This project was supported by USDA CSREES 97-35103-5052, by a special USDA grant to Oregon State University for wood utilization. We thank Roseburg Forest Products, Inc. and Crown Pacific Limited partnership for providing the trees.

References

Dalla-Salda G, Martinez-Meier A, Cochard H, Rozenberg P (2011) Genetic variation of xylem hydraulic properties shows that wood density is involved in adaptation to drought in Douglas-fir (*Pseudotsuga menziesii* (Mirb.)). Ann For Sci 68:747–757

Dean TJ, long JN (1986) Variation in sapwood area-leaf area relations within two stands of lodgepole pine. Forest Sci 32:749–758

Delzon S, Sartore M, Burlett R, Dewar R, Loustau D (2004) Hydraulic responses to height growth in maritime pine trees. Plant Cell Environ 27:1077–1087

Domec J-C, Gartner B (2002) Age and position-related in hydraulic vs. mechanical dysfunction of xylem: inferring the design criteria for Douglas-fir wood structure. Tree Physiol 22:91–104

Domec J-C, Gartner BL (2003) Relationship between growth rates and xylem hydraulic characteristics in young, mature and old-growth ponderosa pine trees. Plant Cell Environ 26:471–483

Domec J-C, Pruyn ML (2008) Bole girdling affects metabolic properties and root, trunk and branch hydraulics of young ponderosa pine trees. Tree Physiol 28:1493–1504

Domec J-C, Pruyn ML, Gartner BL (2005) Axial and radial profiles in conductivities, water storage and native embolism in trunks of young and old-growth ponderosa pine trees. Plant Cell Environ 28:1103–1113

Domec J-C, Meinzer FC, Gartner BL, Woodruff D (2006) Transpiration- induced axial and radial tension gradients in trunks of Douglas-fir trees. Tree Physiol 26:275–284

Domec J-C, Lachenbruch B, Meinzer FC, Woodruff DR, Warren JM, McCulloh KA (2008) Maximum height in a conifer is associated with conflicting requirements for xylem design. Proc Nat Acad Sci USA 105:12069–12074

Domec J-C, Warren J, Lachenbruch B, Meinzer FC (2009) Safety factors from air seeding and cell wall implosion in young and old conifer trees. IAWA J 30:100–120

Domec J-C, Schafer K, Oren R, Kim H, McCarthy H (2010) Variable conductivity and embolism in roots and branches of four contrasting tree species and their impacts on whole-plant hydraulic performance under future atmospheric CO2 concentration. Tree Physiol 30:1001–1015

Ewers FW, Zimmermann MH (1984) The hydraulic architecture of Balsam fir (*Abies balsamea*). Physiol Plant 60:453–458

Gartner BL (2002) Sapwood and inner bark quantities in relation to leaf area and wood density in Douglas-fir. IAWA J 23:267–285

Gonzalez-Benecke CA, Martin TA, Cropper WP (2011) Whole-tree water relations of co-occurring mature *Pinus palustris* and *Pinus elliottii*. Can J For Res 41:509–523

Gould PJ, Harrington CA (2008) Extending sapwood-leaf area ratio relationship from stems to roots in Douglas-fir. Annals For Sci 65:802–880

Greenwood MS, Ward M, Day ME, Adams S, Bond BJ (2008) Age related trends in red spruce foliar plasticity in relation to declining productivity. Tree Physiol 28:225–232

Irvine J, Law BE, Kurpius MR, Anthoni PM, Moore D, Schwarz PA (2004) Age-related changes in ecosystem structure and function and effects on water and carbon exchange in ponderosa pine. Tree Physiol 24:753–763

James S, Meinzer FC, Goldstein G, Woodruff D, Jones T, Restom T, Mejia M, Clearwater M, Campanello P (2003) Axial and radial water transport and internal water storage in tropical forest canopy trees. Oecologia 134:37–45

McCulloh KA, Sperry JS (2005) Patterns in hydraulic architecture and their implications for transport efficiency. Tree Physiol 25:257–267

McCulloh K, Sperry JS, Lachenbruch B, Meinzer FC, Reich PB, Voelker S (2010) Moving water well: comparing hydraulic efficiency in twigs and trunks of coniferous, ring-porous, and diffuse- porous saplings from temperate and tropical forest. New Phytol 186:439–450

McDowell N, Barnard H, Bond BJ et al (2002a) The relationship between tree height and leaf area: sapwood area ratio. Oecologia 132:12–20

McDowell N, Phillips N, Lunch C, Bond BJ, Ryan MG (2002b) An investigation of hydraulic compensation in large Douglas-fir trees. Tree Physiol 22:763–774

Meinzer FC, Woodruff DR, Domec J-C, Goldstein G, Campanello PL, Gatti MG, Villalobos-Vega R (2008) Coordination of leaf and stem water transport properties in tropical forest trees. Oecologia 156:31–41

Mencuccini M (2002) Hydraulic constraints in the functional scaling of trees. Tree Physiol 22:553–565

Ogée J, Brunet Y, Loustau D, Berbigier P, Delzon S (2003) MuSICA, a CO_2, water and Energy multilayer, multileaf pine forest model: evaluation from hourly to yearly time scales and sensitivity analysis. Global Change Biol 9:697–717

Oren R, Waring RH, Stafford S, Barrett JW (1987) Twenty-four years of ponderosa pine growth in relation to canopy leaf area and understory competition. For Sci 33:538–547

Phillips N, Bond BJ, McDowell NG, Ryan MG (2002) Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. Tree Physiol 22:205–211

Phillips N, Bond BJ, McDowell NG, Ryan MG, Schauer A (2003) Leaf area compounds height-related hydraulic costs of water transport in Oregon White Oak trees. Func Ecol 17:832–840

Pruyn ML, Gartner BL, Harmon ME (2003) Stem respiratory potential in six softwood and four hardwood tree species in the central cascades of Oregon. Oecologia 137:10–21

Renninger HJ, Meinzer FC, Gartner BL (2007) Hydraulic architecture and photosynthetic capacity as constraints on release from suppression in Douglas-fir and western hemlock. Tree Physiol 27:33–42

Rosner S, Klein A, Wimmer R, Karlsson B (2006) Extraction of features from ultrasound acoustic emissions: a tool to assess the hydraulic vulnerability of Norway spruce trunkwood? New Phytol 171:105–116

Rosner S, Klein A, Müller U, Karlsson B (2008) Tradeoffs between hydraulic and mechanical stress responses of mature Norway spruce trunk wood. Tree Physiol 28:1179–1188

Ryan MG, Yoder BJ (1997) Hydraulic limits to tree height and tree growth. Bioscience 47:235–242

Ryan MG, Phillips N, Bond BJ (2007) Hydraulic hypothesis limitation revisited. Plant Cell Environ 29:367–381

Schäfer KVR, Oren R, Tenhunen JD (2000) The effect of tree height on crown level stomatal conductance. Plant Cell Environ 23:365–375

Sellin A (1987) Hydraulic conductivity of the water transport system in Norway spruce. Sov Plant Physiol 34:443–449

Sellin A (2001) Hydraulic and stomatal adjustment of Norway spruce trees to environmental stress. Tree Physiol 21:879–888

Simonin K, Kolb TE, Momtes-Helu M, Koch GW (2007) Restoration thinning and influence of tree size and leaf area to sapwood area ratio on water relations of *Pinus ponderosa*. Tree Physiol 26:493–503

Spicer R, Gartner BL (1998) How does a gymnosperm branch assume the hydraulic status of a main stem when it takes over a leader? Plant Cell Environ 21:1063–1070

Spicer R, Gartner BL (2001) The effects of cambial age and position within the stem on specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood. Trees 15:222–229

Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap. Springer, Berlin

Tyree MT, Graham ED, Cooper KE, Bazos LJ (1984) The hydraulic architecture of *Thuja occidentalis*. Can J Bot 61:2105–2111

Van Hees AFM, Bartelink HH (1993) Needle area relationships of Scots pine in the Netherlands. Forest Ecology Manag 58:19–31

Whitehead D, Edwards WRN, Jarvis PG (1984) Relationships between conducting sapwood area, foliage area and permeability in mature *Picea stichensis* and *Pinus contorta* trees. Can J For Res 14:940–947

Williams M, Bond BJ, Ryan MG (2001) Evaluating different soil and plant hydraulic constraints on tree function using a model and sap flow data from ponderosa pine. Plant Cell Environ 24:679–690

Zobel B, Sprague JR (1998) Juvenile wood in forest trees (Springer Series in Wood Science). Springer, NY, p 300