

Axial and radial profiles in conductivities, water storage and native embolism in trunks of young and old-growth ponderosa pine trees

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ABSTRACT

Ponderosa pine has very wide sapwood, and yet the spatial and temporal use of that sapwood for water transport is poorly understood. Moreover, there have been few comparisons of function in tips of old-growth trees in comparison with young trees. In the present study, axial and radial specific conductivity (k_s), leaf specific conductivity (LSC), leaf specific conductance (k_l), native embolism and the compartmentalization of sapwood water storage were characterized in trunks of young and old-growth trees. Trunks of young trees had lower k_s , lower LSC and lower native embolism [corresponding to 5% loss of conductivity (PLC)] than trunks of old-growth trees. However, k_l in young trees was 3.5 times higher than in old-growth trees, supporting the hypothesis that tall trees have a reduced ability to transport water to their leaves. Water storage (capacitance) of young trees was not significantly different than at the base of old-growth trees. Although the top of the old-growth trees had similar k_s , LSC and k_l to the young trees for a given cambial age, they had higher native embolism and lower capacitance. There was no trade-off between k_s and native embolism at any height. In the tree crown, outer sapwood had 35–50% higher k_s than the inner sapwood and 17–25 PLC lower native embolism. At the base of the old trees, there was no significant difference in native embolism between the outer, middle and inner sapwood, showing that refilling of embolisms was complete despite the 130-year difference in wood age among these radial positions. Although during the dry season the inner sapwood tended to be more saturated than the outer sapwood, the outer part of the sapwood contributed up to 60% of the overall stored water. Safer xylem, higher capacitance and higher k_l would appear adaptive in the young trees for regulating their water resource, which is likely to be less reliable than the water availability of older trees with their more developed root system.

Key-words: *Pinus ponderosa*; capacitance; leaf hydraulic conductance; refilling; sapwood; specific conductivity; xylem embolism.

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INTRODUCTION

Within an individual, woody plants have a large radial and vertical variation in the xylem anatomy of their bole (Gartner 1995). Consequently, the top and the bottom of a tree should vary substantially in their hydraulic properties, such as specific conductivity (k_s), water storage and resistance to embolism. Research has shown significant variation in wood k_s with radial position in the trunk, with a maximum usually occurring in the outermost rings and declining towards the heartwood/sapwood boundary because of the changes in xylem anatomy associated with cambial maturation (Granier *et al.* 1994; Spicer & Gartner 2001). In stem sections in which the inner sapwood is older than 30 years cambial age, there should be no further effects of cambial maturation. Because of the physical constraints of working with large trunks, there has been no study examining with accuracy the pattern in k_s in old-growth trees. Such data would clarify the role played by xylem k_s in determining patterns in sap flux density (James *et al.* 2003). Knowledge of radial and vertical k_s would not only improve the understanding of individual trunk functioning, but would also have important implications for modelling water movement to the leaves and assessing the significance of tree age for hydraulic performance (Williams, Bond & Ryan 2001). If these data are combined with sapwood to leaf area ratio (to determine leaf specific conductivity, LSC) and also height (to determine leaf specific conductance, k_l) we can also ask whether for a given cambial age, a young tree has different hydraulic capacity than the top of a big tree.

At the branch level, comparisons of vulnerability to embolism curves, and water potential (Ψ) suggest that *in situ* embolism (defined as the percentage loss of conductivity, PLC) may not influence branch and whole-tree hydraulic conductance (Bond & Kavanagh 1999; Martinez *et al.* 2003). Even though conifer species are able to limit their transpiration rate and trunk Ψ during the dry late summer to prevent partial trunk embolism (Sperry & Pockman 1993; Hacke *et al.* 2000), studies on the main bole showed that trunk sapwood is more vulnerable to embolism than branch sapwood, and that it operates on the edge of hydraulic dysfunction (Domec & Gartner 2002, 2003). In ponderosa pine, a species with wide sapwood, there are significant differences in the vulnerability to embolism

between the top and the bottom of the tree and between young and old-growth trees, but not between the inner and outer sapwood (Domec & Gartner 2003). These vertical patterns of resistance to embolism should exert a strong influence on spatial patterns of water movement in trees.

Water storage capacity, or capacitance, is the ratio of change in water content to change in Ψ . Because wood density varies by location in a tree, it is more accurate to express the capacitance as the ratio of change in relative water content (RWC, the proportion of non-cell wall space that is occupied by water) to change in Ψ of the trunk (Domec & Gartner 2001). Xylem capacitance is correlated with soil to branch hydraulic conductance, sapwood k_s , and resistance to embolism (Meinzer *et al.* 2003; Domec & Gartner 2003). Water withdrawn from capillary spaces, and conduit lumens during daily embolism can enter into the transpiration stream (Lo Gullo & Salleo 1992); presumably, the embolisms are then reversed before water can be withdrawn the next day. The dynamic discharge and recharge of water stored in big trees can be determined accurately by quick direct sampling of the sapwood, using for example, an increment borer (Waring, Whitehead & Jarvis 1979). Estimates of the contribution of stored water to daily transpiration range from 10 to 50% in pine species (Waring *et al.* 1979; Loustau *et al.* 1996). However, the importance of radial partitioning of capacitance between the outer and inner sapwood and the evidence of diurnal variation in sapwood water content are largely unexplored.

The objectives of this study were to determine patterns of trunk conductivities (k_s , LSC and k_1), native embolism and xylem RWC within co-occurring old-growth and young ponderosa pine trees. Our specific objectives included (1) determining whether hydraulic properties differ between a 15-year-old-tree, the top 15 years of an old-growth tree, and an old-growth tree; (2) assessing axial and radial hydraulic properties in k_s , RWC and native embolism within old-growth trees; (3) quantifying the role of the outer sapwood to the whole sapwood capacitance; and (4) learning whether one can combine the vulnerability curves already published (Domec & Gartner 2003) with trunk Ψ to estimate native embolism accurately.

MATERIALS AND METHODS

Plant material, sample preparation and leaf area

The study was performed on private forestland (Crown Pacific Co.) in a mixed-age ponderosa pine stand located near Gilchrist, Oregon, USA (43°32' N; 121°41' W) at elevation 1355 m. The climate was characterized by wet, cool winters and dry, hot summers with an annual mean precipitation of 645 mm (<http://www.orst.edu/Department/IPPC>). The stand was a mix of ponderosa pine and lodgepole pine (*Pinus contorta* Dougl. ex Loud.), ranging from 15 to 300 years old, with approximately 250 trees per hectare on soils derived from deep volcanic ash.

At the end of September 2000, six old-growth trees (243 ± 10 years old, total mean height of 34.1 ± 0.7 m) were selected based on their cambial age at breast height (estimated from increment cores), and their health (free of broken tops, stem deformities or disease). Note that these trees were from the same site as those described in Domec & Gartner (2003), but were taken at a different time and for different objectives. After the trees were felled, four heights of the old-growth trees were sampled, at 1 m above ground (node 240), and at nodes 100 (lower third part of the crown), 50 and 15 counting down from the treetop. The height to each of these sampled nodes was recorded (Table 1). At each height, and from each tree, discs about 15 cm thick were cut, immediately transported in wet polyethylene bags to the laboratory 3 h away, and stored at 3 °C until blocks were prepared within 2 days of felling. Both ends of each disc were in contact with wet paper towels to limit evaporation from the xylem. A thinner second disc was also cut for use in measuring sapwood and heartwood areas. From each of the thick discs, four pairs of 90–110 mm long blocks were taken at regular intervals from the heartwood/sapwood boundary to the outer part of the wood. There were taken in pairs to have a replicate of a given radial position. The blocks were split along the grain first with a maul and wedge, and then with a chisel. The samples were then stored at 3 °C in wet paper towels until they were used within 3 h. At the end of September 2002, nine young

Table 1. Morphological characteristics of young (37 years-old, $n = 9$) and old-growth (243 years-old, $n = 6$) ponderosa pine trees by height position (node) counting down from the treetop, and at the base (about 50 cm from ground, mean ± SE)

Age class	Nodes from top	height (m)	Diameter (cm)	Sapwood area (cm ²)	Heartwood area (cm ²)	Sapwood rings (no.)	Sapwood/leaf area (cm ² m ⁻²)
Young trees	Node 15	2.2 ± 0.5	12.0 ± 1.5	101 ± 29	4 ± 1	14 ± 2	2.8 ± 0.2
	Base	0.5	17.6 ± 1.3	195 ± 33	6 ± 2	31 ± 5	4.4 ± 0.4
Old-growth trees	Node 15	31.9 ± 0.4	5.9 ± 0.8	19.3 ± 2.1	1 ± 1	15 ± 1	2.0 ± 0.2
	Node 50	29.1 ± 1.1	13.3 ± 0.4	119 ± 15	5 ± 1	35 ± 3	2.4 ± 0.3
	Node 100	21.9 ± 1.3	37.8 ± 1.8	827 ± 92	175 ± 33	70 ± 5	2.0 ± 0.2
	Base	0.5 ± 0.1	71.8 ± 5.3	2768 ± 200	701 ± 120	128 ± 6	3.6 ± 0.3
	(Node 240)						

Mean tree heights for old-growth and young trees were 34.1 ± 0.7 m and 5.5 ± 0.6 m, respectively. The base of the live crown averaged a few nodes below node 100 at a mean height of 20 ± 1 m from the ground for old-growth trees, and at 2 ± 1 m from ground for young trees.

trees (Table 1) were randomly selected, felled and a disc taken at node 15 was cut and immediately transported to the laboratory. From each cross-sectional disc, two blocks from the outer part of the wood (because the sapwood was not wide enough to take outer and inner samples) were cut within the same single ring as described above.

Tree leaf area above each sampled node was determined as described by Pruyn, Gartner & Harmon (2002). We divided each tree into two (young trees) or four (old-growth trees) vertical sections. We sub-sampled each section as follows. For sections between nodes 240–100 and nodes 100–50, we kept one-quarter of all shoots, saving every fourth branch (the foliage plus the attached woody material). For the sections between nodes 50–15, nodes 15 to the tip, and young trees, we saved all material. We recorded the fresh mass of the clipped material using spring scales in the field. We then took sub-samples of the clipped material and recorded their fresh mass. We dried the sub-samples, separated leaves from woody twigs and branches and recorded dry mass for each. We also collected 20 needle fascicles from the clipped material from each section and stored them at -10°C , until we were ready to record leaf dimensions with a caliper to calculate leaf area. We then dried the leaves and recorded dry mass. Based on the proportions of leaf area to dry leaf mass, we estimated total all-sided leaf area for each section because ponderosa pine has three-needled fascicles with stomata on all surfaces.

Specific conductivity, leaf specific conductivity, leaf specific conductance and native embolism

Specific conductivity (k_s , in $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) is a measure of the hydraulic efficiency of a unit of xylem and was calculated according to Darcy's law. The efficiency of trunk xylem in conducting water was expressed by the leaf-specific conductivity (LSC in $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$), which is the product of k_s at a given node in the trunk by the sapwood to leaf area ratio measured above the same node. Leaf-specific conductance (k_l , $\text{mol m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) was computed by dividing LSC (after transformation into mole of water for literature comparison) by the height above the node considered. Native PLC was determined by comparing the initial (or native) specific conductivity ($k_{s(i)}$) of trunk segments to the maximum specific conductivity ($k_{s(\text{max})}$) after removal of air emboli by soaking the samples under vacuum for 48 h.

We measured k_s with the membrane-lined pressure sleeve needed to ensure fluid did not leak from the sides of samples (Spicer & Gartner 1998). One end of the pressure sleeve was attached by tubing to a reservoir filled with filtered ($0.22 \mu\text{m}$) water adjusted with HCl to pH 2. It was placed high enough relative to the sample to produce a pressure head of 5.2 kPa, which was a low enough value to avoid refilling of the embolized tracheids. The temperature of the solution was recorded before and after each specific conductivity measurement, and all calculations of k_s were

corrected to 20°C to account for changes in fluid viscosity with temperature. The distal end was attached to a 1-mL micropipette (0.01 mL graduation). When the flow was steady, the time required for the meniscus to cross five consecutive graduation marks was recorded. Samples were 90–110 mm long, with cross-sections ranging from 170 to 190 mm^2 (as determined with the trapezoidal equation based on the height and both widths of each cross section). Percentage loss of conductivity (PLC) was computed as $\text{PLC} = 100(1 - k_{s(i)}/k_{s(\text{max})})$. Following each $k_{s(\text{max})}$ measurement, samples were perfused with filtered ($0.22 \mu\text{m}$) safranin-O (0.2% aqueous solution) under a pressure head of 15 kPa for 20 min while still enclosed in the pressure sleeve apparatus. The samples always stained completely, giving no evidence of embolism.

Trunk and leaf water potential

We determined axial profiles of water potential (Ψ) at five different heights on three old-growth trees from the same site for four consecutive days during summer (19–22 September 2000). To estimate trunk Ψ at the base of the trees, we used temperature-corrected stem psychrometers (Dixon & Tyree 1984; PWS Instruments, Guelph, Ontario, Canada) installed at 1.5 m above the ground on the three mature trees. The sensors were pressed tightly against the sapwood to prevent loss of contact from diurnal swelling of bark and cambium. We used a CR7X data logger (Campbell Scientific Inc., Logan, UT, USA) to take measurements every half hour.

Leaf Ψ was estimated at three heights within the crown, corresponding to nodes 15, 50, and 100, counting down from the top (determined from cores taken with an increment borer) with a pressure chamber (PMS Instruments Co., Corvallis, OR, USA) on three foliage-bearing branch cuttings per tree and per height every 15 min for 3 h at mid-day (Ψ_{leaf}). Trunk Ψ at predawn (Ψ_{predawn}) and midday (Ψ_{midday}) at the same three heights was estimated by making pressure chamber measurements every 15 min for 2–3 h on foliage-bearing branch cuttings bagged to prevent transpiration (Begg & Turner 1970). Additionally, we estimated Ψ_{predawn} , Ψ_{midday} and Ψ_{leaf} on the lowest branch possible on each of the three trees (corresponding roughly to node 180, at an average height of 9.9 m).

From March 2000 to March 2002, we used the pressure chamber to estimate Ψ_{predawn} and Ψ_{leaf} every 4–6 weeks from six randomly selected old-growth trees from the same site and of the same general size and form as the harvested ones used for hydraulic measurements. On the same days and at the same site, we also estimated the seasonal change in Ψ_{predawn} , Ψ_{midday} and Ψ_{leaf} at node 15 in the trunks of six young trees (37 years old), using the pressure chamber techniques described above.

Trunk relative water content

We made *in situ* axial profiles of RWC of trunk wood from increment cores (12 mm in diameter) on the same days and

on the same three old-growth trees on which we measured axial profiles of trunk Ψ . We collected the cores at predawn and between 1300 and 1500 h solar time at midday. For the lowest three heights, we split the sapwood portion. We split the cores into four segments at the base, three segments at node 100 and two segments at node 50. For the top core of the old-growth trees and for the young trees (node 15), we used the entire sapwood for one measurement. We determined the heartwood/sapwood boundary visually. Because of the small diameter of their trunks, we could take increment cores only 5 mm in diameter from the young trees. We wrapped each core in plastic film and put it in a vial while we were up in the tree, but we split and recorded the fresh weight of each core (M_f) within 10 min of harvest. Back at the laboratory, we determined V_f (fresh volume) by water displacement and M_d (dry mass) for the cores. Assuming a cell-wall material density of 1.53 g cm^{-3} (Siau 1984), RWC was calculated as $\text{RWC} = (M_f - M_d)/(V_f - M_d/1.53)$.

Additionally, to obtain the winter trend in RWC, we made a vertical profile on six other old-growth trees harvested from the same site in March 2000. For the seasonal pattern, we collected cores at midday every 4–6 weeks from March 2000 to March 2002 on six other old-growth and six young trees. We collected the cores on the same days that we measured Ψ_{predawn} and Ψ_{leaf} , and determined RWC as described above.

Seasonal trunk depletion at each sapwood depth was calculated by taking the difference between RWC at a given date and maximum RWC measured during the year. Total trunk depletion was calculated by weighting the values by the proportion of the sapwood area occupied by each of the sapwood depths. That way, we could also determine the contribution of each sapwood depth to the total sapwood depletion, and normalize it by the area of sapwood represented by each depth. Capacitances were calculated by dividing the daily loss in RWC between predawn and midday by the difference between trunk Ψ_{predawn} and Ψ_{midday} .

Predicted native embolism

For the old-growth trees, measured PLC within the bole was compared with PLC derived from trunk Ψ_{midday} and published vulnerability curves constructed in the laboratory on six different trees from the same site (Domec & Gartner 2003). For the young trees, the pieces of trunk sampled to determine native embolism and $k_{s(\text{max})}$ were used to establish new vulnerability to embolism curves. Vulnerability curves were established using the air injection method (Sperry & Saliendra 1994) adapted for trunkwood samples (Domec & Gartner 2001). For the young trees, we decided to re-determine vulnerability curves and not use the already published vulnerability curves because the latter were made on younger and smaller trees (Domec & Gartner 2003). Moreover, to better compare with the native embolism values, it allowed us to determine the predicted native embolism at the field trunk Ψ_{midday} experienced by each of the nine trees felled.

Statistical analysis

We used least squares methods to fit relationships between hydraulic parameters. The values of k_s , LSC, k_i , RWC, and native PLC, were compared among trunk locations by carrying out an analysis of variance (ANOVA) using a strip-plot randomized complete block design (trees as block) with radial position and height position being the strip plots factors. The experiment was designed to assess values at different sapwood depths, but for height position we were interested in an estimate of the entire sapwood. Therefore, the effect of height position on the parameters was made by weighting the values by the proportion of the total sapwood area occupied by each of the sapwood depths. We determined differences in hydraulic parameters and field measurements between old-growth and young trees by means of a one-way ANOVA. To assess the difference at the base of the old-growth trees between outer, middle and inner sapwood at each date, we used a two-way ANOVA with one repeated measure factor. We performed all statistical procedures with Statistical Analysis Systems software (1999; SAS Inc., Cary, NC, USA).

RESULTS

Water potential and relative water content between young and old-growth trees

The leaf water potential and trunk relative water content of the young trees were similar to the base of the old-growth trees. The seasonal Ψ_{predawn} showed only a 0.5 MPa change between the least negative values (winter) and the most negative values (after 3 months without rain) for either old-growth or young trees (Fig. 1). The average minimum Ψ_{leaf} never fell below about -2.1 MPa in either old-growth or young trees. In young trees, in which we were able to measure Ψ_{leaf} and bagged leaf water potential as a surrogate of trunk water potential (trunk Ψ_{midday}) throughout the seasons, the difference between those values was about 0.4 MPa throughout the entire summer with a minimum trunk Ψ_{midday} never falling below -1.3 MPa. During the summer, the driving force in the trunk, or difference between trunk Ψ_{predawn} and Ψ_{midday} ranged between 0.5 and 0.8 MPa in the young trees. Within the old-growth trees, the driving force increased from 0.4 MPa at the base to 0.6 MPa at the top. These values were not significantly different ($P > 0.22$) than the driving force in the young trees (0.6 MPa) at the same period. However, the resulting driving force gradient (corrected for gravitational component) was 10 times higher in the young trees (0.1 MPa m^{-1}) than in the old-growth trees (0.01 MPa m^{-1}). Additionally, the trunk Ψ_{midday} of the young trees in September 2000 (when the old-growth trees were felled) and in 2002 (when the young trees were felled) were not significantly different ($P > 0.51$).

Relative water content (RWC) at breast height followed the same trend as trunk Ψ_{midday} , but had higher variation in young trees than in old trees, in spite of similarly negative water potentials (Fig. 1). Seasonal sapwood RWC taken at

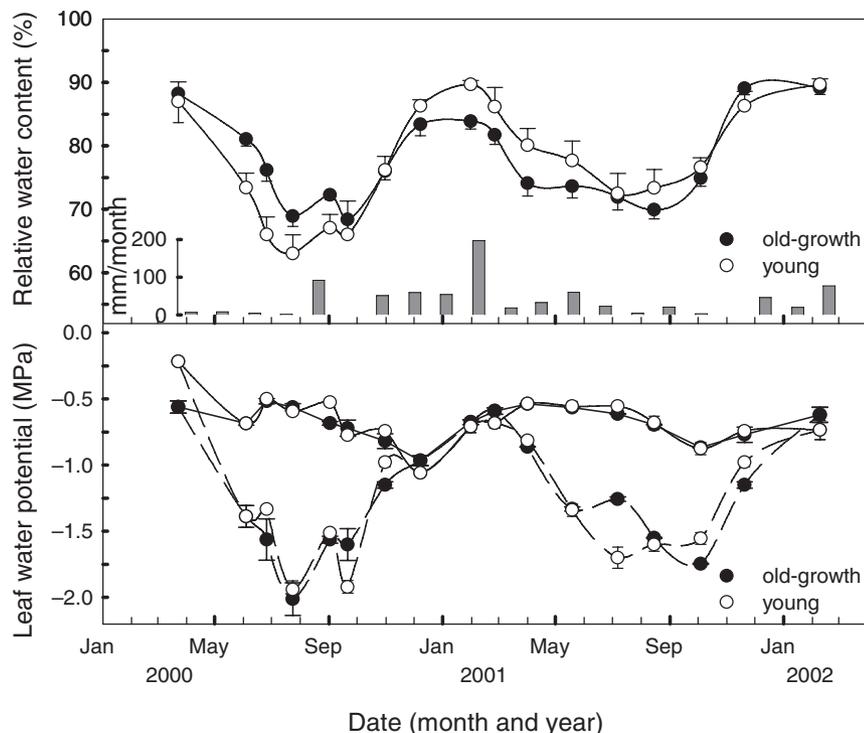


Figure 1. Temporal change in sapwood RWC taken at midday and leaf water potential (corrected for the hydrostatic gradient of 0.01 MPa m^{-1}) taken at predawn (solid lines) and at midday (dashed lines) for old-growth and young ponderosa pine trees over two consecutive years. Histograms represent the monthly precipitation recorded 5 km from the study site. Error bars are standard errors.

midday at breast height in either young or old-growth trees was positively related to Ψ_{midday} (Table 2), but was not correlated with Ψ_{predawn} (data not shown).

Comparisons in trunk $k_{s(\text{max})}$, PLC, native LSC, native k_1 and RWC between young and old trees

Sapwood thickness averaged 185 mm at the base for the old-growth trees and 44 mm at node 15 (close to the base) for the young trees. At node 15 in the young trees, $k_{s(\text{max})}$ ($2.7 \pm 0.3 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$) was not significantly different ($P = 0.56$) than at node 15 in the old-growth trees (Table 3). Just before felling the young trees, the trunk Ψ_{midday} was -1.4 MPa , which resulted in only 5 PLC (Table 3). The top trunk of old-growth trees, node 15, experienced higher PLC than did the trunk of the young trees at the same node (Table 3). By taking into account the native PLC, the native LSC at node 15 in the young trees ($6.9 \pm 0.4 \times 10^{-4} \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$) was not significantly different ($P = 0.22$) than at node 15 in the old trees but was significantly three times lower ($P = 0.01$) than at the base of the old-growth trees (Table 3). The native k_1 at the base of the old-growth trees was 3.5 times lower than k_1 at the top (node 15) and than k_1 of the young trees ($P < 0.03$). The native k_1 between the young trees and the top of the old-growth trees were not statistically different ($P = 0.4$, Table 3).

At the base of the old-growth trees, the average daily change in RWC ($7.5 \pm 2.7\%$) for the summer measurements was comparable with the total change ($6.4 \pm 2.5\%$) between the winter and the summer predawn values. In young trees however, the daily decrease in RWC was as low as 9.1 ± 3.3

(Table 3), compared with a seasonal decrease of 15–20% (Fig. 1). The calculated water storage (capacitance) using the daily change in RWC and differences between trunk Ψ_{predawn} and Ψ_{midday} at node 15 (close to the base) in the young trees was $20\% \text{ RWC MPa}^{-1}$ and was significantly higher ($P = 0.01$) than the xylem capacitances at node 15 in the old-growth trees, but was not significantly different ($P = 0.31$) than at the base of the old-growth trees (Table 3).

Radial profiles of RWC, $k_{s(\text{max})}$ and native PLC within the trunk of the old-growth trees

At the base of the old-growth trees, $k_{s(\text{max})}$ varied gradually from $5.2 \pm 0.3 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ in the innermost sapwood to $6.8 \pm 0.6 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ in the outermost sapwood

Table 2. Slopes (a) and intercepts (b) of the linear regressions of the sapwood relative water content (RWC) versus the leaf water potential (Ψ_{leaf}) measured in the field at midday (corrected for the hydrostatic gradient of 0.01 MPa m^{-1}) for the old-growth and the young trees ($\text{RWC} = a\Psi_{\text{leaf}} + b$, $P < 0.001$ in every case)

Age class	a	b	r^2
Old-growth trees			
Outer sapwood	$14.5 \pm 2.4 \text{ a}$	$96 \pm 2 \text{ a}$	0.70
Middle sapwood	$11.6 \pm 2.1 \text{ ab}$	$90 \pm 3 \text{ ab}$	0.66
Inner sapwood	$9.5 \pm 1.9 \text{ b}$	$87 \pm 3 \text{ b}$	0.62
Young trees	$16.0 \pm 3.3 \text{ a}$	$97.7 \pm 4 \text{ a}$	0.63

Values with different letters within a column are significantly different ($P < 0.05$).

Table 3. Maximum specific conductivity ($k_{s(\max)}$), native leaf-specific conductivity (LSC), native leaf-specific conductance (k_l), native percent loss of $k_{s(\max)}$ (native PLC), relative water content (RWC) measured at predawn and midday and capacitance at the base of the old-growth (base) and the young trees (node 15), and at the top of the old-growth trees (node15)

Age class	$k_{s(\max)}$ ($\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)	LSC ($10^{-4} \text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$)	k_l ($10^{-2} \text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)	Native PLC	RWC (%)		Capacitance (%RWC MPa^{-1})
					predawn	midday	
Old-growth							
base	6.2 ± 0.5 a	19.7 ± 2.0 a	0.33 ± 0.02 a	12.9 ± 1.1 a	81 ± 4 a	73 ± 3 a	22.3 ± 2.1 a
node 15	3.2 ± 0.4 b	5.6 ± 0.7 b	1.28 ± 0.16 b	13.1 ± 0.9 a	62 ± 2 b	59 ± 2 b	5.9 ± 0.9 b
Young							
node 15	2.7 ± 0.3 b	6.9 ± 0.4 b	1.11 ± 0.07 b	5.2 ± 1.0 b	73 ± 3 a	65 ± 3 a	20.2 ± 2.9 a

Values with different letters within a column are significantly different ($P < 0.05$).

(Fig. 2a). At any given height, outer sapwood in the old-growth trees always had significantly higher $k_{s(\max)}$ than inner sapwood ($P < 0.05$). The largest differences occurred at node 50 and node 100 with a 51 and a 47% increase between outer and inner sapwood, respectively (Fig. 2a).

The lower part of the crown, nodes 50 and 100, had a significantly higher ($P < 0.04$) native PLC than the base and the top (Fig. 2b). At the base of the trunk, radial native PLC and RWC did not differ significantly ($P > 0.34$) from the inner to the outer sapwood (Fig. 2c). In the tree crown however (nodes 50 and 100), an increase in native PLC from the inner to the outer sapwood was associated with a decrease in RWC. The tree base and the lower part of the crown (node 100) had significantly higher ($P < 0.03$) RWC than the upper two heights (Fig. 2c).

Radial partitioning of water storage at the base of the old-growth trees

At the breast height in the old-growth trees RWC was always lower for the inner sapwood than for the outer sapwood in the winter and spring ($P < 0.04$, Fig. 3a), but reached the same values ($70 \pm 1.3\%$) in the late summer. As a consequence the difference between outer and inner sapwood varied from a maximum value of 8% in winter to around 0% in at the end of the summer (Fig. 3b). The rates of decreasing RWC between April and July and increasing RWC between October and February were faster in the outer sapwood than in the inner sapwood (Fig. 3a). If one sums the monthly decreases in RWC from February to the end of September, one finds that the cumulative depletion of water in the breast height discs corresponded to 15–19% of the discs' total sapwood RWC. The amount of seasonal trunk water depletion was dependent on rainfall events and increased as months without significant rainfall occurred (Fig. 3b).

During the growing season, from April to October, outer sapwood contributed more than 57% to the total trunk water depletion, compared with 31 and 12% for the middle and inner sapwood, respectively (Fig. 4a). The magnitude of storage was always higher in the outer sapwood than in the middle and inner sapwood combined. Compared to the volume represented by each layer, water storage from the

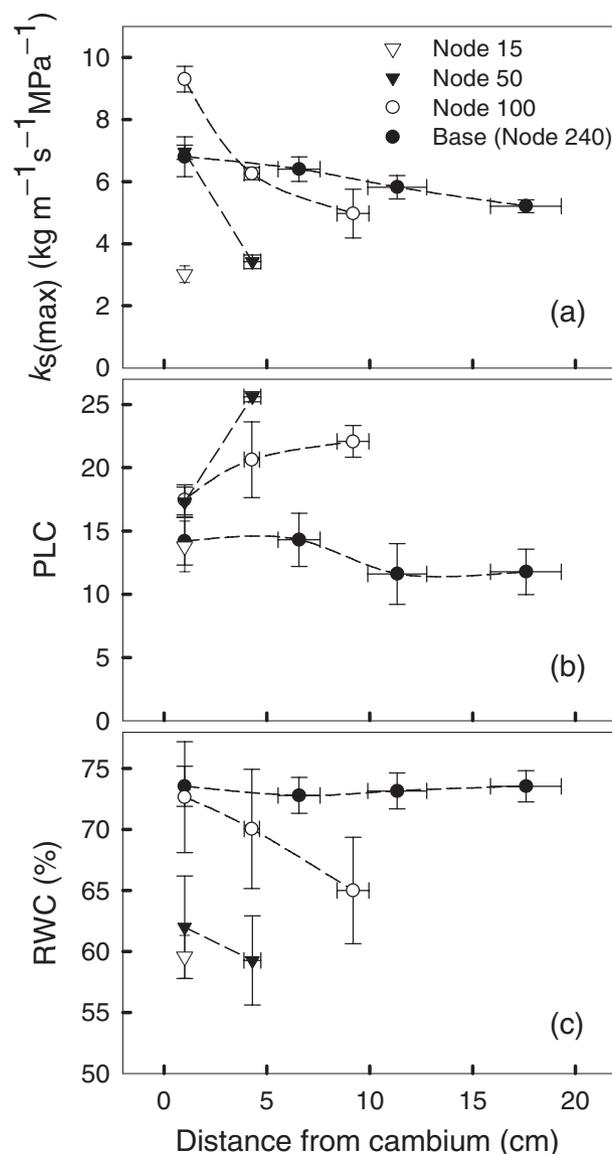


Figure 2. (a) Hydraulic specific conductivity ($k_{s(\max)}$) measured at full water saturation (b) percentage loss of hydraulic conductivity (PLC), and (c) relative water content (RWC) taken at midday versus the distance from cambium at four different heights in the trunks of old-growth ponderosa pine trees. Error bars are standard errors.

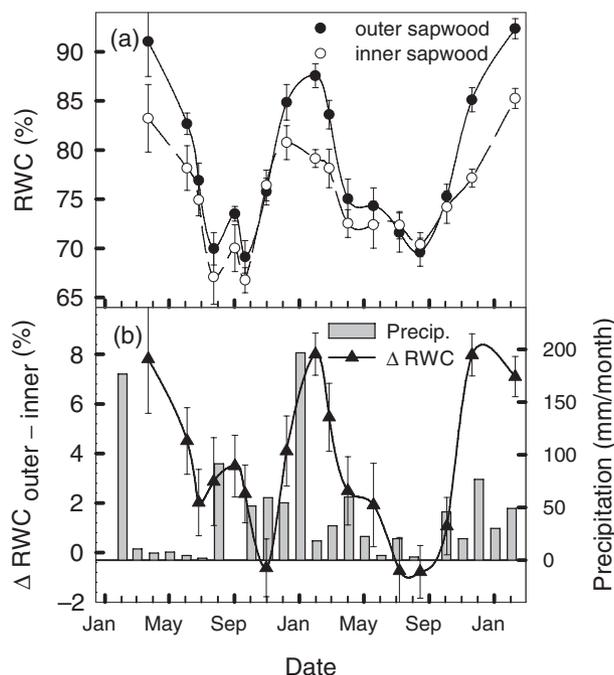


Figure 3. Temporal change in (a) relative water content (RWC) in outer and inner sapwood, and in (b) the difference in RWC between outer and inner sapwood (Δ RWC) in old-growth ponderosa pine trees over two consecutive years at breast height. Error bars are standard errors.

outer sapwood contributed up to 40% more than its volume, whereas the middle sapwood contributed roughly in proportion to its volume, and inner sapwood contributed 50% less than its proportional volume (Fig. 4b).

Axial profiles in water potentials, RWC, $k_{s(\max)}$, native PLC, LSC and k_l in the old-growth trees

In the old-growth trees, trunk Ψ_{predawn} and Ψ_{midday} decreased linearly from bottom to top (Fig. 5a). For the summer predawn measurements, the slope of the curve of Ψ_{predawn} by height did not differ significantly from the hydrostatic slope ($P = 0.62$). The slopes for Ψ_{midday} and Ψ_{leaf} values were 36 and 19% higher than the hydrostatic gradient, respectively ($P < 0.02$), but did not differ significantly from one another ($P = 0.11$). Similar to the pattern with trunk Ψ_{midday} , RWC decreased from treetop to tree bottom, but this decrease was not linear (Fig. 5b). Unlike at the tree base, the average daily change in RWC ($3.3 \pm 1.9\%$) for the summer measurements at the treetop was lower than the total change ($11.4 \pm 3.1\%$) between the winter and the summer predawn values. The calculated capacitance decreased linearly from 22 to 6% RWC MPa⁻¹ between the bottom to the top of the old-growth trees (Fig. 6).

Using the averaged values from each disc, $k_{s(\max)}$ in the old-growth trees decreased linearly in the crown going up the tree from $7.3 \pm 0.4 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ (node 100) to $3.2 \pm 0.4 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ (node 15). There were significantly higher ($P < 0.03$) values of PLC at the top (nodes 100

and 50) than at the base in the inner sapwood (20 PLC versus 12 PLC), but not in the outer sapwood (Fig. 7a). We used vulnerability curves and trunk Ψ_{midday} to predict the PLC for old-growth trees and found that the predicted PLC values were substantially lower ($P = 0.02$) than the measured PLC values (Fig. 7a & b). However, the shapes of the curve with height were similar between predicted and measured. The predicted values did not differ significantly ($P = 0.48$) from the measured values in the young trees (Fig. 7b). As a consequence of no differences in sapwood/leaf area by height (Table 1), and similar values of native PLC, native LSC decreased significantly ($P < 0.03$) in the crown going up the tree from $11.4 \pm 1.1 \times 10^{-4} \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ (node 100) to $5.6 \pm 0.7 \times 10^{-4} \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ (node 15). On the other hand, because of the height factor, native k_l increased significantly ($P < 0.01$) in the crown from $0.42 \pm 0.05 \times 10^{-2} \text{ mol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ (node 100) to $1.28 \pm 0.16 \times 10^{-2} \text{ mol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ (node 15), respectively.

DISCUSSION

Comparing water transport between young and old-growth trees

Our study indicates that although values of water potentials and trunk capacitances were similar across age classes,

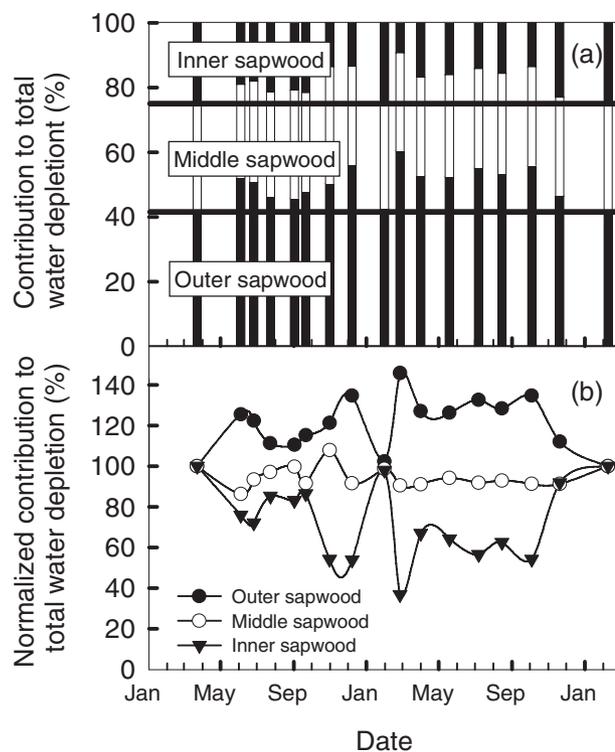


Figure 4. Temporal change in (a) the contribution and (b) the normalized contribution to total sapwood water depletion among the outer, middle and inner sapwood at breast height. The thick horizontal lines represent the volume of wood represented by each layer. The normalized contribution is the contribution divided by the volume of wood that each layer represented.

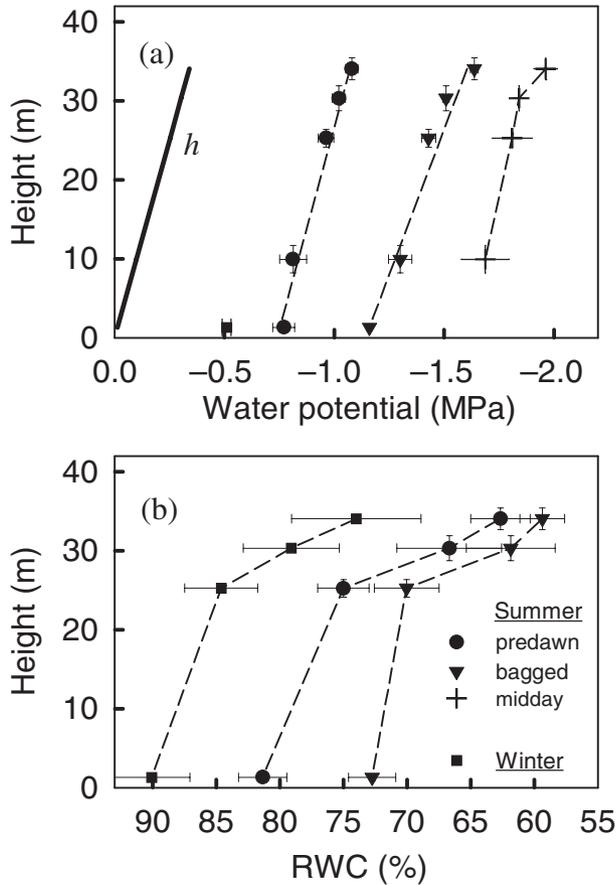


Figure 5. Height in old-growth ponderosa pine trees versus (a) leaf and trunk water potentials, and (b) relative water content (area-weighted average of values from outer, middle and inner sapwood). Values are for winter (filled squares), summer trunk predawn (filled circles), and summer trunk midday (filled triangles). In (a), the solid line represents the theoretical hydrostatic gradient ($h = 0.01 \text{ MPa m}^{-1}$, plotted through the origin). The crosses (leaf) represent the water potential for summer midday data of unbagged leaves. Error bars are standard errors.

$k_{s(\text{max})}$, native LSC and native PLC, in young trees were lower than in old-growth trees. Water flow is determined by the water potential gradient from soil to leaf, the conductivity and the capacitance of the xylem. 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, which is a surrogate of the real capacity of the xylem to supply water to leaves. However, this vascular advantage did not compensate for tree size. Even though the xylem of the old-growth tree was more efficient at transporting water, the young trees had a higher k_1 than the old-growth trees, consistent with studies using transpiration and water potential to determine k_1 (McDowell *et al.* 2002; Delzon *et al.* 2004). We can predict that because the decline in k_1 with tree height was not compensated by an increase in soil-to-leaf water potential difference (Fig. 1), whole tree water

flux per leaf area would also be significantly lower in the old-growth trees than in the young trees (Ryan *et al.* 2000).

By contrast, this trend did not hold when comparing the top of the old-growth trees to the young trees. Values of k_s , LSC, and k_1 were indistinguishable between wood in the young trees and the same-aged (node 15) tips of old-growth trees. Therefore, moving water within the soil to a young tree seems to be as hard as moving water from the lower to the upper part of a tall tree. It is logical to infer that the higher capacitance of the young trees compared to the top of the old-growth trees might buffer for higher below-ground resistance when soil dries due to an increase in root embolism. Indeed, it has been shown that native root embolism is higher in young trees than in old-growth trees (Jaquish & Ewers 2001; Domec *et al.* 2004).

A trade-off existed at the base of the trunks between k_s and PLC between the young and old-growth trees. Higher conductivity in the old-growth trees was at the cost of higher native embolism than in the young trees. Our data also showed that trunk Ψ_{midday} was maintained above a common minimum threshold of -1.2 MPa values in either the base of the young or old-growth trees. This trunk homeostasis regulation followed the maintenance of a common Ψ_{leaf} at around -2.1 MPa between young and old-growth trees. This concordance suggests that despite probable differences in maximum rooting depth and water use among tree age, there was a degree of convergence in trunk Ψ_{midday} thresholds at which trunk embolism accelerates and stomata begin to regulate Ψ_{leaf} (Hacke *et al.* 2000).

Irvine & Grace (1997) reported changes in the diameter of the sapwood due to tension within the xylem of Scots pine. In the current study such contractions may have occurred in old-growth and young trees. We found that RWC can decrease daily as much as 5% below the crown and 8% at the base of the old-growth trees (Table 3; Fig. 5b), and 9% in the young trees. For the young trees, this change represents a loss of only 1.1 kg of water. For the

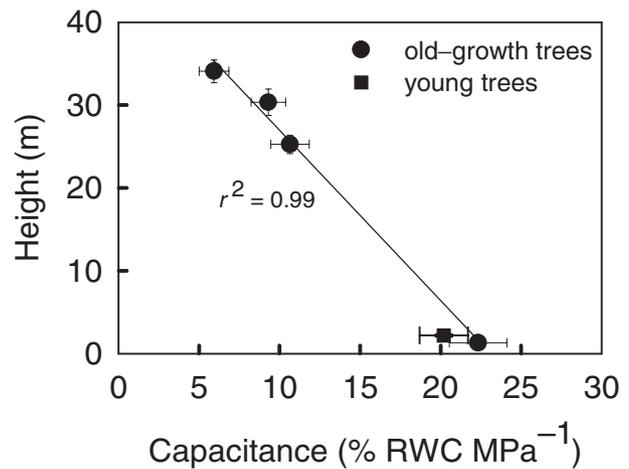


Figure 6. Height in old-growth ponderosa and young pine trees versus summer daily water storage (capacitance). Error bars are standard errors.

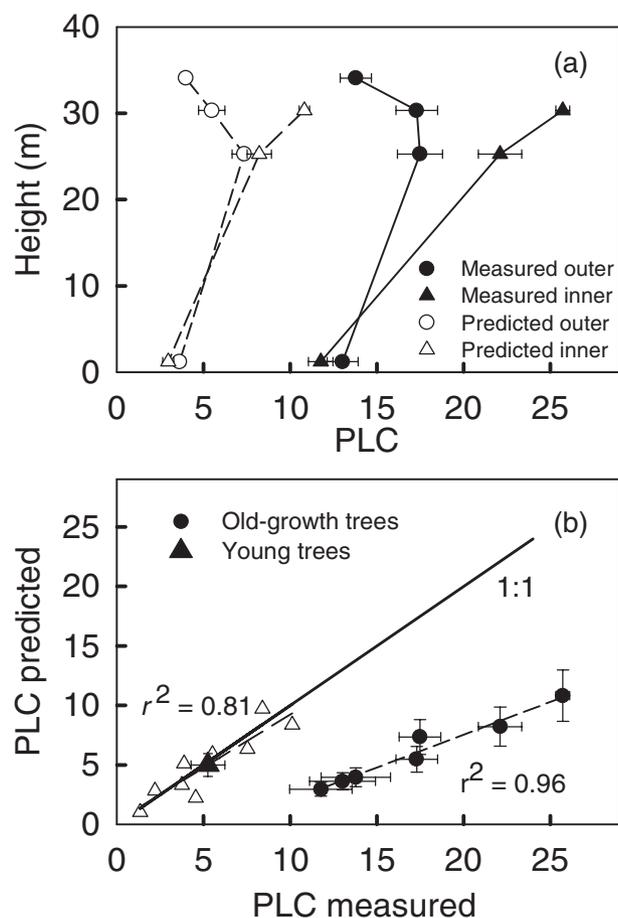


Figure 7. (a) Measured (filled symbols) and estimated (open symbols), from vulnerability curves (Domec & Gartner 2003) and from trunk water potentials shown in Fig. 5a, percent loss of conductivity (PLC) with height in old-growth ponderosa pine trees. (b) Measured and estimated PLC in young (filled triangles) and old-growth (filled circles) trees. Open triangles represent the data for each of the nine individual small trees.

old-growth trees with large sapwood, the daily change in trunk RWC represents a net daily water loss of about 152 kg. If this loss is compared with the potential maximum daily water use of 185 kg for this species (measured on a nearby site on similar-sized trees, Irvine *et al.* 2002; Phillips *et al.* 2003), such a sapwood discharge represents 79% of the total daily water use, which is substantially more than the 10–30% usually calculated when using sap flow measurements (Loustau *et al.* 1996; Goldstein *et al.* 1998; Phillips *et al.* 2003). Between August and September, the trunk RWC decreased by 0.2% diurnally, which represents a daily trunk water depletion of 6–7 kg. This daily change in trunk RWC suggests that deriving water storage by the instantaneous difference between the sap flow recorded at the base and at the top of the tree may underestimate the total capacitance of the bole. Indeed, these sap flow techniques assume a zero night flow, even though there is increasing evidence of significant nocturnal transpiration in many

woody species (Bucci *et al.* 2004). This daily loss of water content contributes substantially to the total water storage capacity, which would be about 4% of the tree's total transpiration. Such results should be considered in research studying the reliance of trees on stored water because the 24 h sum of crown water flux does not equal bole water flux. For species with large sapwood, small diurnal changes in RWC result in a large amount of water exchanged that represents trunk water deficit and not trunk water storage when not replenished at night.

Trade-offs between spatial variation in RWC, k_s and native PLC within the old-growth trees

We now have evidence that the main bole, and especially its outer part, plays an adaptive role in preserving the whole tree hydraulic integrity. The main contribution of stored water came from the outer part of the sapwood rather than the middle or inner sapwood. Additionally, sapwood at the tree base had a higher daily change in RWC than did sapwood at the top of the tree, resulting in a much higher capacitance at the tree base, which buffered the decreased in k_i .

If we define juvenile wood as samples ≤ 20 rings from the pith, and mature wood as samples with ≥ 35 rings from the pith (Abdel-Gadir & Kraemer 1993), the $k_{s(\max)}$ of juvenile wood was 20–30% lower than mature wood ($P < 0.001$). In conifers this pattern has been reported (Spicer & Gartner 2001; Domec & Gartner 2002) and suggested in studies comparing $k_{s(\max)}$ at the same height in the trunk for different silvicultural regimes (Pothier *et al.* 1989), or different age classes (Mencuccini & Comstock 1997). Within the individual, juvenile wood had 30–40% higher native embolism than mature wood. We know of no other data to have compared these locations. Sap flux density has often been reported to vary throughout the sapwood, peaking at 2 cm from the cambium and declining toward the heartwood (reviewed in Gartner & Meinzer 2005). Contrary to this sharp decline in sap flux density from bark to pith at the base of the trees, we showed only a slight decrease in $k_{s(\max)}$. Sap flux density and $k_{s(\max)}$ might not be linearly related which may reveal the existence of radial water potential gradients (James *et al.* 2003; Domec *et al.* in press).

A small trade-off existed at the base of the trunk between $k_{s(\max)}$ and resistance to xylem embolism. Although our results showed that there was little difference in $k_{s(\max)}$ at the base of the old-growth trees, decreasing values of $k_{s(\max)}$ between the outer, middle and inner part of sapwood were associated with a small, but not a significant, decrease in PLC. In both angiosperms and gymnosperms, evidence of a trade-off has been found within trees (Salleo & Lo Gullo 1989; Domec & Gartner 2001, 2003). On the other hand, higher native embolism under the live crown (node 100) was not correlated with higher $k_{s(\max)}$ (Fig. 2a & b). On the contrary, axial and radial $k_{s(\max)}$ appeared to be positively related to native embolism in the upper trunk. More intriguing was that at the base of the trunk, native PLC and RWC did not differ significantly between outer and inner

sapwood (Fig. 2b & c). These results showed that refilling of embolism occurred during the 130-years difference in wood age between these radial positions.

The trunk base of the old-growth trees and above all the trunk wood of along the branched part operated at around or at more negatives values than the air entry points for embolism defined by Domec & Gartner (2001). The air entry points, calculated to be at 12 PLC when vulnerability curves are sigmoidal, denote the points where runaway embolism begins and the edge of xylem dysfunction for water transport (Tyree & Sperry 1988). The base of the old-growth trees averaged 13 PLC with a trunk Ψ_{midday} of -1.2 MPa, which supports results from Jackson, Irvine & Grace (1995) who measured by acoustic emissions embolism at the base of mature Scots pine trees occurred for Ψ as high as -1.3 MPa. The higher PLC measured in the inner sapwood of the upper part of the tree have only a small effect on hydraulic functioning of the trees because these parts represent a small proportion of the total sapwood (because of the small diameter), and can be compensated by 20–25% increase in sapwood area each year. At the bottom of the trees, inner and middle sapwood account for 40% of the total area, and therefore the trees cannot afford high embolism because one more year of growth will only increase the area by 2–4% (Domec & Gartner 2003).

Measured versus estimated loss of conductivity

Within the old-growth trees, the native values of PLC of the present study were higher than the values we predicted using vulnerability curves and trunk Ψ_{midday} , although they followed the same trend with height (Fig. 7b). Perhaps this offset in the curves is caused by the air injection method altering the refilling behavior compared to embolism induced in the field by water stress (Salleo *et al.* 1992). The mechanism responsible for refilling embolized xylem conduits is still unknown, but refilling is faster when embolism is artificially induced by air pressure than when it is naturally induced by drought. The increased susceptibility of xylem to cavitation as a result of prior cavitation, defined as cavitation fatigue, and the hysteresis in the refilling processes have been recently proposed to explain the discrepancy between measured and predicted PLC from vulnerability curves (Hacke & Sperry 2003). Measured and predicted PLC in young trees agreed well in comparison with the old-growth trees. This result is not due to the young sapwood age measured, because the outer sapwood within the old-growth trees was also young and yet showed a discrepancy between measured and calculated PLC.

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