

Effects of branch height on leaf gas exchange, branch hydraulic conductance and branch sap flux in open-grown ponderosa pine

ROBERT M. HUBBARD,^{1–3} BARBARA J. BOND,⁴ RANDY S. SENOCK⁵ and MICHAEL G. RYAN^{1,2}

¹ USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO 80526, USA

² Colorado State University, Graduate Degree Program in Ecology, Fort Collins, CO 80523, USA

³ Author to whom correspondence should be addressed (rhubbard@sparc.ecology.uga.edu)

⁴ Oregon State University, 154 Peavy Hall, Corvallis, OR 97331, USA

⁵ College of Agriculture, Forestry and Natural Resource Management, 200 W. Kawili Street, University of Hawaii, Hilo, HI 96720, USA

Received February 26, 2001; accepted October 26, 2001; published online May 1, 2002

Summary Recent studies have shown that stomata respond to changes in hydraulic conductance of the flow path from soil to leaf. In open-grown tall trees, branches of different heights may have different hydraulic conductances because of differences in path length and growth. We determined if leaf gas exchange, branch sap flux, leaf specific hydraulic conductance, foliar carbon isotope composition ($\delta^{13}\text{C}$) and ratios of leaf area to sapwood area within branches were dependent on branch height (10 and 25 m) within the crowns of four open-grown ponderosa pine (*Pinus ponderosa* Laws.) trees. We found no difference in leaf gas exchange or leaf specific hydraulic conductance from soil to leaf between the upper and lower canopy of our study trees. Branch sap flux per unit leaf area and per unit sapwood area did not differ between the 10- and 25-m canopy positions; however, branch sap flux per unit sapwood area at the 25-m position had consistently lower values. Branches at the 25-m canopy position had lower leaf to sapwood area ratios ($0.17 \text{ m}^2 \text{ cm}^{-2}$) compared with branches at the 10-m position ($0.27 \text{ m}^2 \text{ cm}^{-2}$) ($P = 0.03$). Leaf specific conductance of branches in the upper crown did not differ from that in the lower crown. Other studies at our site indicate lower hydraulic conductance, sap flux, whole-tree canopy conductance and photosynthesis in old trees compared with young trees. This study suggests that height alone may not explain these differences.

Keywords: leaf specific conductance, *Pinus ponderosa*, photosynthesis, sap flow, stomatal conductance.

Introduction

Stomata are responsive to changes in hydraulic conductance of the flow path from soil to leaf. Leaf specific hydraulic conductance (K_L) of whole plants has been positively related to stomatal conductance, because K_L changes with development (Meinzer and Grantz 1990, Saliendra et al. 1995, Mencuccini and Grace 1996, Hubbard et al. 1999) and between species

(Meinzer et al. 1995). Stomata also respond to experimental manipulations of hydraulic conductance involving induction of xylem cavitation (Sperry and Pockman 1993), root pruning (Teskey et al. 1983, Meinzer and Grantz 1990), notching of stem xylem (Sperry et al. 1993), freeze-thawing of stems (Hammel 1967) and defoliation (Pataki et al. 1998, Hubbard et al. 1999). More recently, Hubbard et al. (2001) showed that both stomatal conductance and photosynthesis varied linearly with K_L in ponderosa pine (*Pinus ponderosa* Laws.) seedlings. The response occurs within minutes of the manipulation of hydraulic conductance, and bulk leaf water status can remain nearly constant during the experiment (Teskey et al. 1983, Sperry and Pockman 1993, Saliendra et al. 1995, Hubbard et al. 2001).

These studies suggest a tight link between liquid and vapor phase conductances arising from stomatal control of plant water status. Stomatal control allows photosynthesis, but at the same time must prevent dehydration-induced damage from excessive transpiration. Preventing dehydration-induced damage requires that stomata close below a critical leaf water potential, thereby preventing cavitation of the water column (Tyree and Sperry 1988, Jones and Sutherland 1991). Because changes in hydraulic conductance can alter flow and thus plant water status, stomata respond to changes in K_L , although the specific mechanism remains unknown.

The K_L in trees depends on the path length from soil to leaf (Pothier et al. 1989), suggesting that g_s may also vary with tree height. Whitehead et al. (1984) proposed a simple hydraulic model to illustrate the interrelationships between sapwood permeability (k), the pressure difference between the ends of the flow path ($\Delta\Psi$), leaf area (A_l), sapwood area (A_s), air saturation deficit (D), stomatal conductance (g_s), path length (l) and viscosity (η):

$$\frac{A_l}{A_s} = \frac{k(\Delta\Psi)}{l\eta Dg_s} \quad (1)$$

Rearrangement of Equation 1 to solve for stomatal resistance ($r_s = 1/g_s$) gives:

$$r_s = \frac{A_1}{A_s} \frac{l\eta D}{k(\Psi_{\text{soil}} - \Psi_{\text{leaf}})}. \quad (2)$$

This model suggests that r_s will be proportional to the length of the flow path unless there are changes in A_1/A_s , sapwood permeability, $\Delta\Psi$ or some combination thereof. Schäfer et al. (2000) recently used a similar hydraulic model to explain variations in whole-canopy conductance (G_c) with height in European beech (*Fagus sylvatica* L.). Changes in A_1/A_s in their study partially compensated for the effects of height on g_s . Other investigators have found that A_1/A_s measured at breast height declines with increasing tree height (see review by McDowell et al. 2002). In general, a decrease in A_1/A_s with tree height may mitigate the effects of increased path length by decreasing the ratio of transpirational to transport tissues.

Few studies have examined the effects of increased height on K_L , g_s and A within a single tree canopy. The length of the flow path from soil to leaf can vary substantially in trees with deep canopies with potentially large differences in g_s and K_L between the top and bottom of the tree. Because most studies examining leaf-level gas exchange with canopy depth have focused on changes in microclimate or light interception (e.g., Ellsworth and Reich 1993, Schoettle and Smith 1999, Rijkers et al. 2000), there is little information on the direct effect of canopy height on leaf-level gas exchange. Understanding how height within the canopy of open-grown trees affects stomatal conductance and photosynthesis may improve mechanistic models of tree and forest growth and response to climate change.

Whitehead et al. (1984) showed that their hydraulic model also explained differences in stem internode A_1/A_s and the foliage above the internode within a single tree. However, because there is good evidence that resistance in branches can be much greater than in the stem (Zimmermann 1983, Tyree and Ewers 1991, Yang and Tyree 1994), it is possible that branch A_1/A_s may be an equally important hydraulic adjustment to increased path length from the bottom to the top of the canopy.

Our objective was to assess the impact of branch height on branch A_1/A_s , K_L (from soil to end of branch ($K_{L,\text{tree}}$) and branch only ($K_{L,\text{branch}}$)), sap flux, r_s , photosynthesis (A) and the foliar $\delta^{13}\text{C}$ ratio in ponderosa pine growing in an open stand on the east side of the Oregon Cascades. We reasoned that the increased length of the flow path from the bottom to the top of the canopy would cause proportional differences in branch sap flux, r_s , A and K_L , and that these parameters may be affected by changes in the A_1/A_s ratio of branches with height.

Materials and methods

The study site is located near Black Butte, Oregon (44°25' N 121°40' W) at an elevation of 1030 m. Many years of partial thinning and harvesting have resulted in an open stand (LAI < 1) of ponderosa pine with most trees receiving full sunlight

throughout the day. The old, tall trees at our site are about 36 m tall and 290 years old. There is a sparse understory consisting of bitterbrush (*Purshia tridentata* (Pursh) DC.), snowbrush (*Ceanothus velutinus* Doug.), manzanita (*Arctostaphylos patula* Greene) and several species of bunch grass. The soil is a deep sandy loam derived from volcanic ash and classified as a light-colored andic Inceptisol.

Winters at Black Butte are cool and wet, whereas summers are warm and dry, and most precipitation falls during winter. Mean annual precipitation is 360 mm with about 17% falling between May and September (Oregon Climate Service, Oregon State University, Corvallis, OR).

Gas exchange measurements

We used two methods of canopy access for our gas exchange measurements. We erected scaffolding beside one tree (T1) to a height of 25 m allowing access to the upper and lower third of the canopy. For this tree, we measured leaf gas exchange on six branches each at heights of 10 and 20 m on Days 190, 191, 194 and 195. We used a hydraulic lift to access the upper and lower third of three other ponderosa pine trees (T2–T4). Using the lift, we measured leaf gas exchange on four branches each at heights of ~10 and 25 m on Days 202, 203 and 204.

Gas exchange measurements were made with an LI-6400 (Li-Cor, Lincoln, NE) open system infrared gas analyzer (Field et al. 1989). We measured r_s , transpiration (E) and A on 1-year-old intact needles in natural, saturating, photosynthetically active radiation (PAR > 1000 $\mu\text{mol m}^{-2}$) (Hadley 1969). Relative humidity and CO_2 concentration within the chamber were kept near ambient using the automated control of the LI-6400. Branches were exposed to full sunlight for at least 30 min before measurement. We measured relative humidity (for calculation of air saturation deficit) and PAR at a 10-m tower about 50 m from the study trees. Temperature and relative humidity were measured with a CS500 (Campbell Scientific, Logan, UT) and PAR was measured with a Li-Cor LI-190SB quantum sensor.

Branch sap flux measurements

We measured branch sap flux (F) in the canopy of T1 with heat balance sap flux gauges as described by Senock and Ham (1993). We measured 10 branches at heights of both 10 and 25 m. Branches were chosen that received full sunlight for the longest part of the day. In a separate study at our site, there was no statistical difference in diurnal light flux density between the top and bottom of the crown where our sap flux measurements were taken (B.J. Bond, personal communication). Sap flux gauges were installed on branches approximately 2 cm in diameter as described by Senock and Ham (1993) and each gauge was insulated with polyurethane foam and wrapped with aluminum foil to protect the gauge from solar radiation.

We calculated F (kg s^{-1}) as:

$$F = (Q - Q_v - Q_r) / (c(T_{\text{so}} - T_{\text{si}})), \quad (3)$$

where Q is heat energy supplied to the gauge, Q_v is apical and basal heat energy transferred by conduction along the stem

axis, Q_r is radial conduction of energy perpendicular to the branch axis, c is specific heat of water ($\text{J kg}^{-1} \text{K}$) and $T_{\text{so}} - T_{\text{si}}$ is the temperature difference between the water flowing into and out of the heated segment.

Sap flux measurements were collected each minute, averaged, and stored every 15 min (21X data logger, Campbell Scientific). We measured branch Q from 0300 to 2100 h on Days 191–211. We estimated heat loss from conduction (Q_r) on a humid night prior to Day 191, assuming zero flow through the branches. For the measurement period, we turned off the power from 2100 through 0300 h to conserve battery power (charged with solar panels). Sap flux is expressed per unit projected leaf area (F_L ; m^2) and per unit sapwood area (F_{sw} ; cm^2).

Carbon isotope composition measurements

If increased resistance reduces water supply to the foliage in the upper canopy, photosynthesis will be limited more by stomatal conductance than by enzymatic capacity for photosynthesis. Therefore, foliage from the upper crown should show less discrimination to ^{13}C than foliage from the lower crown in these open, well-ventilated canopies and the $\delta^{13}\text{C}$ value of the cellulose in upper canopy foliage should be greater than that of the lower canopy (cf. Evans et al. 1986, Farquhar et al. 1989). We extracted cellulose from 1-year-old foliage on branches from the upper and lower canopy of our sample trees as described by Wise et al. (1945). The extracted cellulose was analyzed by mass spectrometry at the Stable Isotope Facility at the University of Waikato, New Zealand.

Soil to leaf conductance

We estimated conductance from soil to leaf (K_{Ltree}) for 1-year-old needles at the top and bottom of trees T2–T4 as:

$$K_{\text{Ltree}} = g_s D / (\Psi_{\text{soil}} - \Psi_{\text{leaf}}). \quad (4)$$

We estimated Ψ_{soil} from predawn Ψ_{leaf} measurements corrected for the hydrostatic gradient. We measured g_s and Ψ_{leaf} on two branches between 1100 and 1300 h.

Branch conductance

After measuring gas exchange for trees T2–T4, we destructively sampled two branches from the upper and lower canopy per tree (25 and 10 m). Branch lengths averaged 0.92 m (SE = 0.1) and 0.94 m (SE = 0.1) from the 25- and 10-m canopy positions, respectively, whereas branch diameter averaged 19.4 cm (SE = 1.3) and 19.3 cm (SE = 0.15). We recut the branches under water and transported them to the laboratory with cut ends immersed in water.

In the laboratory, each branch was connected to a potometer and allowed to transpire at low PAR ($\sim 400 \mu\text{mol m}^{-2}$). After steady-state flow was reached (~ 30 minutes), Ψ_{leaf} was measured on three fascicles and branch resistance (K_{Lbranch}) calculated as:

$$K_{\text{Lbranch}} = F / \Delta P, \quad (5)$$

where F is the flow of water through the branch (ml min^{-1}), ΔP is the difference between Ψ_{leaf} and Ψ of water in the potometer reservoir exposed to the atmosphere.

Leaf and sapwood area

We sampled 10 branches per canopy position for T1 and two branches per canopy position for trees T2–T4 (as part of the K_{Lbranch} measurements). After the respective measurements on the intact branches were completed, branch needles were harvested, dried at 65°C for 48 h and weighed. Projected leaf area was determined from a leaf area versus biomass relationship developed at the same site (Ryan et al. 2000).

After K_{Lbranch} was determined for trees T2–T4, functional and total sapwood area (cm^2) were measured in a 5-cm section taken from the proximal end of the branch. We connected the segment to a gravity flow system with a pressure head of 0.01 MPa and allowed filtered ($0.22 \mu\text{m}$) 0.1% (w/v) safranin dye (Sperry and Sullivan 1992) to flow through the segment. When the dye appeared on the distal end of the segment, we removed a thin disk from the middle of the segment and measured the total and stained sapwood area with an image analysis system (Image Pro, Media Cybernetics, Silver Spring, MD).

Data analysis

Differences in the relationship of leaf gas exchange to D were assessed by averaging r_s , E and A by 0.25- D class for all trees and measurement days. We analyzed the response of leaf gas exchange to D with a general linear model (Neter et al. 1990). The individual branch was our sampling unit, but because we measured leaf gas exchange on the same branch throughout each day we used a repeated measures analysis. This analysis assumes a constant correlation among measurements on the same tree branch (a standard compound symmetric covariance model).

We used two relationships to assess differences in branch sap flux with height ($n = 10$ branches for each height in T1). First, we estimated the average diurnal pattern by computing hourly means for each gauge over the measurement period. Second, we estimated the response of F_L and G_i to D by averaging all gauges by 0.25-kPa increments for all the days during the measurement period. For both relationships, we assessed differences by functional analysis of variance (Ramsey and Silverman 1997). For this test, there was no violation of the assumptions of normality and homogeneity of variance.

Because we turned off the power at night, we were unable to assess the role of capacitance in our assumption that $F_L = E$ for our derivation of G_i . However, in a study that included tree T1, Ryan et al. (2000) found that the effect of capacitance on F_L was small ($\sim 12\%$) and did not affect diurnal patterns of sap flux in ponderosa pine at our study site.

For each branch we assumed $F_L = E$ and calculated whole-branch conductance (G_i) as:

$$G_i = F_L / D, \quad (6)$$

where F_L is xylem sap flux per unit leaf area and D is air saturation deficit in partial pressure units (kPa). Branch G_t represents the conductance of the average leaf on the branch. Although G_t includes both branch conductance (g_{branch}) and aerodynamic conductance (g_a) (Köstner et al. 1992), we assumed that G_t roughly equals g_{branch} because these ponderosa pine canopies are well coupled to the atmosphere and g_a is typically at least an order of magnitude greater than g_{branch} in coniferous forests (Lindroth 1985, Granier et al. 1996).

Differences in $K_{L\text{tree}}$ and $K_{L\text{branch}}$ were determined by functional analysis of variance (Ramsay and Silverman 1997). For A_1/A_s ($n = 4$), $K_{L\text{tree}}$ and $K_{L\text{branch}}$ ($n = 3$), the tree was our sampling unit.

Results

The response of r_s and A to D did not vary with canopy height ($P = 0.83$ and 0.34 , respectively) (Figures 1A and 1B). Minimum r_s was $6.9 \text{ m}^2 \text{ s mol}^{-1}$ and maximum A was about $16 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$. At high D , r_s increased to about $18.6 \text{ m}^2 \text{ s mol}^{-1}$ and A declined to about $6 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$. The linear correlation coefficients (r) for r_s and A versus D at both canopy positions were 0.82 and 0.66 , respectively.

Branch sap flux and total branch conductance showed little variation with canopy height. Mean diurnal F_L did not vary between the upper and lower canopy ($P = 0.62$) (Figure 2). Al-

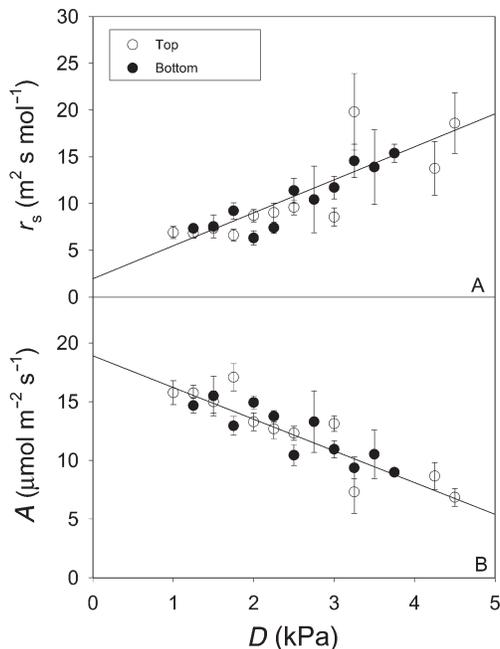


Figure 1. Stomatal resistance (r_s) (A) and net photosynthetic assimilation (A) (B) versus air saturation deficit (D) by canopy position for three ponderosa pine trees at the Black Butte study site. All measurements were averaged by $0.25\text{-}D$ class increments. The response of foliage from the upper and lower canopy did not differ for r_s ($P = 0.82$) or A ($P = 0.35$). The r^2 for r_s was 0.43 and 0.46 in the upper and lower canopy, respectively. The r^2 for A was 0.44 and 0.51 in the upper and lower canopy, respectively. Error bars are ± 1 SE.

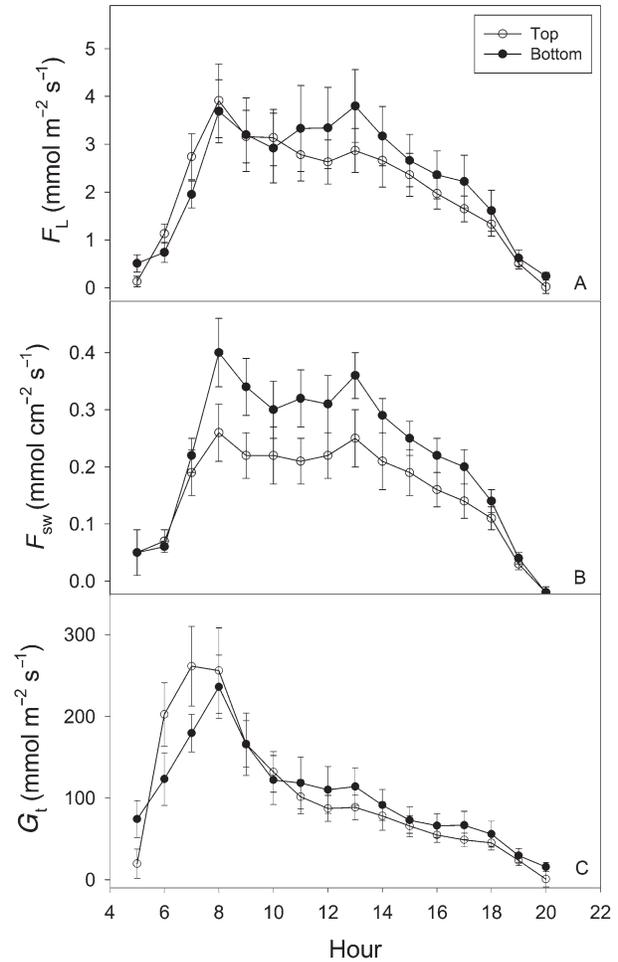


Figure 2. Mean hourly branch sap flux per unit leaf area (F_L), per unit sapwood area (F_{sw}) and mean hourly branch conductance (G_t) for Days 191–211. Fifteen-minute values were averaged by hour for Days 191–211. Differences with canopy position were not significant for any of the parameters ($P = 0.62$, 0.12 and 0.98 for F_L , F_{sw} and G_t , respectively). Error bars are ± 1 SE.

though diurnal F_{sw} was consistently lower at 25 m than at 10 m , the differences were not significant ($P = 0.12$) (Figure 2). Mean F_L increased steadily in the morning, fluctuated around a maximum value of about $3.5 \text{ mmol m}^{-2} \text{ s}^{-1}$ during late morning and early afternoon and then steadily declined later in the day (Figure 2). Mean diurnal G_t peaked around 0800 h , steadily declined throughout the day (Figure 2) and did not differ with branch height in the canopy ($P = 0.90$). The responses of branch sap flux and total branch conductance to D were similar to those with canopy height. Mean F_L peaked around 1.75 kPa for both upper and lower canopy positions and remained relatively constant at higher D ($P = 0.41$) (Figure 3). Although G_t was slightly greater for upper-canopy branches than for lower-canopy branches at low D values, the differences were not significant ($P = 0.77$) (Figure 3).

The $\delta^{13}\text{C}$ values also did not vary with canopy height ($P = 0.88$). The $\delta^{13}\text{C}$ of 1-year-old needles was -22.99 and -23.04‰ for the upper and lower canopy, respectively. Leaf

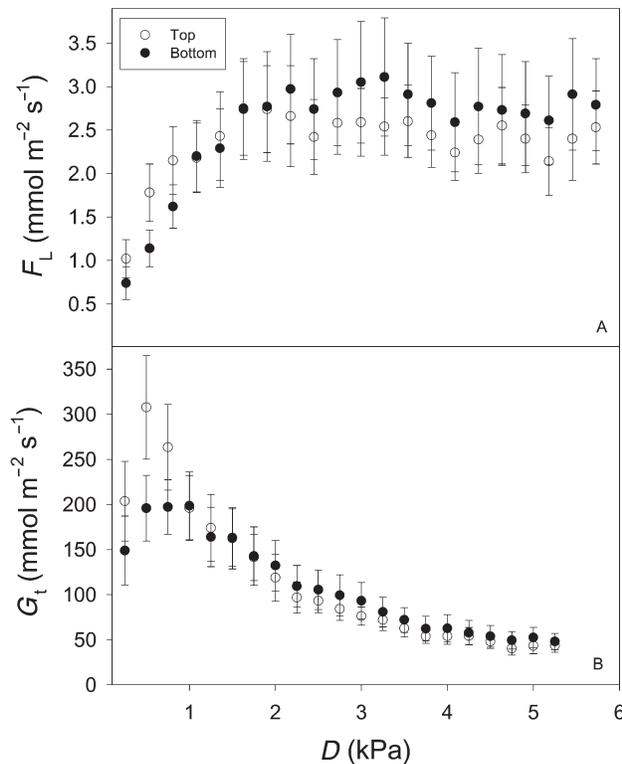


Figure 3. Mean hourly sap flux per unit leaf area (F_L) and whole-branch conductance (G_t) versus D for Days 191–211. Fifteen-minute values were averaged by 0.25-kPa class. There was no significant difference with canopy position for either parameter ($P = 0.41$ and 0.77 for F_L and G_t , respectively). Error bars are ± 1 SE.

nitrogen concentration was also similar in the upper and lower canopy ($\sim 1.2\%$) ($P = 0.75$).

Neither K_{Ltree} nor $K_{Lbranch}$ changed with canopy height ($P = 0.56$ and 0.48 , respectively). The values of $K_{Lbranch}$ were 0.14 and 0.11 $\text{kg h}^{-1} \text{MPa}^{-1} \text{m}^{-2}$ at the top and bottom of the canopy, respectively, and the corresponding values for K_{Ltree} were 0.14 and 0.15 $\text{kg h}^{-1} \text{MPa}^{-1} \text{m}^{-2}$ (Figure 4A).

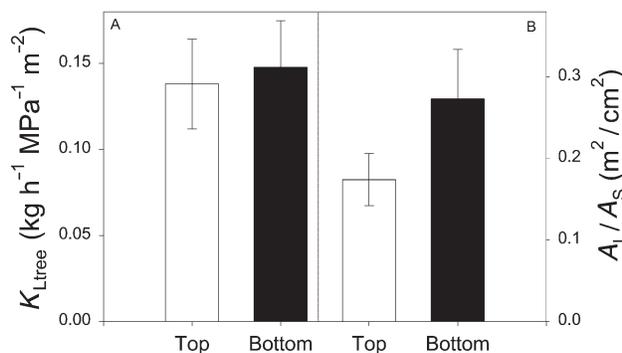


Figure 4. Mean leaf specific conductance (branch only) (K_{Ltree}) (A) and mean leaf to sapwood area ratio A_l/A_s (B) at the top and bottom of the canopy. Values of K_{Ltree} did not differ with canopy position ($P = 0.48$) and A_l/A_s was significantly lower at the top of the canopy than at the bottom of the canopy ($P = 0.03$). Error bars are ± 1 SE.

The leaf area to sapwood ratio varied significantly with canopy height, with branches at ~ 25 m exhibiting a significantly lower A_l/A_s than branches at ~ 10 m (0.17 versus 0.27 $\text{m}^2 \text{cm}^{-2}$; $P = 0.03$) (Figure 4B).

Discussion

The soil to leaf pathway for branches in this study was slightly more than twice as long for upper branches than for lower branches. The Whitehead model (Equation 2) predicts that r_s will be higher in the upper canopy than in the lower canopy unless k_s , $\Delta\Psi$ or A_l/A_s change in concert with path length. We measured Ψ_{leaf} and Ψ_{soil} for a subset of our gas exchange measurements to estimate K_{Ltree} for trees T2–T4 and found no difference in $\Delta\Psi$ with canopy height after accounting for gravitational potential (0.01 MPa m^{-1}). We did not measure permeability directly, but neither branch functional sapwood nor hydraulic conductance varied with canopy height. Assuming no difference in $\Delta\Psi$ or k (and allowing A_l/A_s to vary with height), we predicted r_s for branches at 10 and 25 m with Equation 2. The r_s predicted with the Whitehead model did not differ from measured r_s ($P = 0.36$). Values of $K_{Lbranch}$ and K_{Ltree} also did not differ with canopy height ($P = 0.56$ and 0.48 , respectively). Taken together, these data suggest that decreased branch A_l/A_s with branch height completely compensates for either increased path length or some other variable that changes in concert with path length (e.g., greater branch length or increased number of branch junctions) in these trees.

Most other studies that have examined leaf gas exchange throughout a canopy profile have focused on the light environment of the foliage in closed-canopy forests (e.g., Ellsworth and Reich 1993, Schoettle and Smith 1999, Rijkers et al. 2000). However, Cochard et al. (1997) examined the vertical profile of leaf gas exchange in 15 – 18 -m tall ash trees (*Fraxinus excelsior* L.) growing in an open stand and found little variation in g_s and E with canopy position. Likewise, Oliveira et al. (1996) found that g_s did not vary with crown position in cork oak (*Quercus suber* L.). These data are consistent with the patterns we observed, but the cause cannot be attributed to changes in A_l/A_s because this parameter was not measured in either of the earlier studies.

Branch sap flux and total branch conductance showed little variation with canopy height ($P = 0.62$) (Figure 2), providing independent support for the lack of variation in leaf gas exchange with crown position. The responses of branch sap flux and total branch conductance to D were also unaffected by canopy height. However, F_{sw} was consistently lower at 25 m than at 10 m, although the differences were not significant ($P = 0.12$). This suggests that lower leaf area per unit sapwood area in the upper branches maintains similar water supply per unit leaf area. Our estimate of G_t (mean stomatal conductance of the branch) also indicates that vapor phase conductance does not differ with canopy height.

The $\delta^{13}\text{C}$ signature of foliage provides a time-integrated measure of plant water status (Farquhar et al. 1989, Warren and Adams 2000). Under similar environmental conditions, $\delta^{13}\text{C}$ signature of foliage in the upper canopy should be higher

(less negative) than in the lower canopy if lower K_L at the top of the canopy reduces g_s and A . Stable isotope carbon values did not vary with canopy height ($P = 0.88$). The $\delta^{13}\text{C}$ of 1-year-old needles was -22.99 and -23.04‰ for the upper and lower canopy, respectively. Because $\delta^{13}\text{C}$ was unaffected by foliage position, we suggest that this provides further evidence of similarity of r_s (and consequently A) with canopy position.

At our site, open-grown ponderosa pine trees appear to mitigate the effects of increased path length from soil to leaf by reducing A_1/A_s in upper-canopy branches. Oren et al. (1986) also found lower A_1/A_s ratios in upper versus lower canopy branches in *Picea abies*. Kaufmann (1995), who examined differences in growth patterns between high- and low-vigor ponderosa pine growing near Flagstaff, AZ, used a branch sapwood to leaf area relationship from five crown positions to estimate total leaf area. Although these specific data were not published, an initial analysis indicated a linear decline in branch A_1/A_s with height ($P < 0.01$), supporting our findings.

How the shift in branch A_1/A_s occurs suggests that plants have different mechanisms for dealing with increased hydraulic constraints with height growth. There are few studies examining branch-level changes in A_1/A_s with height, but Cochard et al. (1997) found that branch leaf area declined in the upper canopy of *Fraxinus excelsior* trees presumably in response to increased xylem resistance. In our study, differences in branch diameter were small and not statistically different, allowing us to compare the relative amounts of leaf area and sapwood per branch in the upper and lower canopy. We found that leaf area decreased from 0.7 to 0.5 m^2 and sapwood area increased from 2.4 to 3.6 cm^2 from the bottom to the upper canopy; however, neither of these changes was significant. The argument that changes in A_1/A_s result solely from decreased leaf area or increased sapwood quickly becomes circular. In our study trees, both parameters seemed to change in concert, leading to lower branch A_1/A_s in the upper canopy.

Although we observed no difference in branch gas exchange, sap flux and hydraulic conductance with height within a tree, there are differences in these parameters between tall and short trees at our site. Hubbard et al. (1999) found lower K_L and a steeper decline in g_s and A with D at the tops of tall versus short ponderosa pine at the Black Butte site, and Ryan et al. (2000) showed that whole-tree sap flux and canopy gas exchange were also lower in the tall trees. Our data suggest that height alone is not the dominant factor explaining differences in hydraulic conductance and leaf gas exchange between tall and short trees. Other factors, such as changes in the tortuosity of the flow path, increased number of branch junctions, changes in root or leaf surface area, root permeability or vulnerability to cavitation, may dominate. Future studies should implement an integrative approach that employs simultaneous measurements of canopy gas exchange and water use of large and small trees while accounting for possible compensatory mechanisms like changes in A_1/A_s of boles and branches.

Acknowledgments

Thanks to Dave Woodruff for field assistance, Rudy King for help

with the statistical analysis and Merrill Kaufmann for providing branch A_1/A_s data. Funding for this research was provided in part by USDA-NRICGP-9401021 awarded to Barbara Bond and Michael G. Ryan

References

- Cochard, H., M. Peiffer, K. Le Gall and A. Granier. 1997. Developmental control of xylem hydraulic resistances and vulnerability to embolism in *Fraxinus excelsior* L.: impacts on water relations. *J. Exp. Bot.* 48:655–663.
- Ellsworth, D.S. and P.B. Reich. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* 96:169–178.
- Evans, J.R., T.D. Sharkey, J.A. Berry and G.D. Farquhar. 1986. Carbon isotope discrimination measured concurrently with gas exchange to investigate CO_2 diffusion in leaves of higher plants. *Aust. J. Plant Physiol.* 13:281–292.
- Farquhar, G.D., J.R. Ehleringer and K.T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol.* 40:503–537.
- Field, C.B., J.T. Ball and J.A. Berry. 1989. Photosynthesis: principles and field techniques. *In Plant Physiological Ecology: Field Methods and Instrumentation*. Eds. R.W. Pearcy, J.R. Ehleringer, H.A. Mooney and P.W. Rundel. Chapman and Hall, New York, pp 209–252.
- Granier, A., P. Biron, B. Köstner, L.W. Gay and G. Najjar. 1996. Comparisons of xylem sap flow and water vapour flux at the stand level and derivation of canopy conductance for Scots pine. *Theoret. Appl. Climat.* 53:115–122.
- Hadley, E.B. 1969. Physiological ecology of *Pinus ponderosa* in Southwestern North Dakota. *Am. Mid. Nat.* 81:289–315.
- Hammel, H.T. 1967. Freezing of xylem sap without cavitation. *Plant Physiol.* 42:55–66.
- Hubbard, R.M., B.J. Bond and M.G. Ryan. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiol.* 19:165–172.
- Hubbard, R.M., V. Stiller, M.G. Ryan and J.S. Sperry. 2001. Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant Cell Environ.* 24:113–121.
- Jones, H.G. and R.A. Sutherland. 1991. Stomatal control of xylem embolism. *Plant Cell Environ.* 14:607–612.
- Kaufmann, M. 1995. To live fast or not: growth, vigor and longevity of old-growth ponderosa pine and lodgepole pine trees. *Tree Physiol.* 16:139–144.
- Köstner, B.M.M., E.-D. Schulze, F.M. Kelliher, D.Y. Hollinger, J.N. Byers, J.E. Hunt, T.M. McSeveny, R. Meserth and P.L. Weir. 1992. Transpiration and canopy conductance in a pristine broad-leaved forest of *Northofagus*: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia* 91:350–359.
- Lindroth, A. 1985. Canopy conductance of coniferous forests related to climate. *Water Resour. Res.* 21:297–304.
- McDowell, N., H. Barnard, B.J. Bond, et al. 2002. The relationship between tree height and leaf area:sapwood area ratio. *Oecologia*. In press.
- Meinzer, F.C. and D.A. Grantz. 1990. Stomatal and hydraulic conductance in growing sugarcane: stomatal adjustment to water transport capacity. *Plant Cell Environ.* 13:383–388.
- Meinzer, F.C., G. Goldstein, P. Jackson, N.M. Holbrook, M.V. Butierrez and J. Cavelier. 1995. Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic conductance properties. *Oecologia* 101:514–522.

- Mencuccini, M. and J. Grace. 1996. Developmental patterns of above-ground hydraulic conductance in a Scots pine (*Pinus sylvestris* L.) age sequence. *Plant Cell Environ.* 19:939–948.
- Neter, J., W. Wasserman and M.H. Kutner. 1990. Applied linear statistical models: regression, analysis of variance and experimental design. Irwin, Boston, MA, 547 p.
- Oliveira, G., C. Werner and O. Correia. 1996. Are ecophysiological responses influenced by crown position in cork-oak? *Ann. Sci. For.* 53:235–241.
- Oren, R., K.S. Werk and E.-D. Schulze. 1986. Relationships between foliage and conducting xylem in *Picea abies* (L.) Karst. *Trees* 1: 61–69.
- Pataki, D.E., R. Oren and N. Phillips. 1998. Responses of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. *J. Exp. Bot.* 49:871–878.
- Pothier, D., H.A. Margolis, J. Poliquin and R.H. Waring. 1989. Relation between the permeability and the anatomy of jack pine sapwood with stand development. *Can. J. For. Res.* 19:1564–1570.
- Ramsay, J.O. and B.W. Silverman. 1997. Functional data analysis. Springer-Verlag, Berlin, 310 p.
- Rijkers, T., T.L. Pons and F. Bongers. 2000. The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. *Funct. Ecol.* 14:77–86.
- Ryan, M.G., B.J. Bond, B.E. Law, R.M. Hubbard, D. Woodruff, E. Cienciala and J. Kucera. 2000. Transpiration and whole-tree conductance in ponderosa pine trees of different heights. *Oecologia* 124:553–560.
- Saliendra, N.Z., J.S. Sperry and J.P. Comstock. 1995. Influence of leaf water status on stomatal response to humidity, hydraulic conductance, and soil drought in *Betula occidentalis*. *Planta* 196: 357–366.
- Schäfer, K.V.R., R. Oren and J.D. Tenhunen. 2000. The effect of tree height on crown level stomatal conductance. *Plant Cell Environ.* 23:365–377.
- Schoettle, A.W. and W.K. Smith. 1999. Interrelationships among light, photosynthesis and nitrogen in the crown of mature *Pinus contorta* ssp. *latifolia*. *Tree Physiol.* 19:13–22.
- Senock, R.S. and J.T. Ham. 1993. Heat balance sap flow gauge for small diameter stems. *Plant Cell Environ.* 16:593–601.
- Sperry, J.S. and W.T. Pockman. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. *Plant Cell Environ.* 16:279–287.
- Sperry, J.S. and J.E.M. Sullivan. 1992. Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species. *Plant Physiol.* 100:605–613.
- Sperry, J.S., N.N. Alder and S.E. Eastlack. 1993. The effect of reduced hydraulic conductance on stomatal conductance and xylem cavitation. *J. Exp. Bot.* 44:1075–1082.
- Teskey, R.O., T.M. Hinckley and C.C. Grier. 1983. Effect of interruption of flow path on stomatal conductance of *Abies amabilis*. *J. Exp. Bot.* 34:1251–1259.
- Tyree, M.T. and F.W. Ewers. 1991. The hydraulic architecture of trees and other woody plants. *Tansley Review No. 34. New Phytol.* 119:345–360.
- Tyree, M.T. and J.S. Sperry. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiol.* 88:574–580.
- Warren, C.R. and M.A. Adams. 2000. Water availability and branch length determine $\delta^{13}\text{C}$ in foliage of *Pinus pinaster*. *Tree Physiol.* 20:637–643.
- Whitehead, D., W.R.N. Edwards and P.G. Jarvis. 1984. Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. *Can. J. For. Res.* 14:940–947.
- Wise, L.F., M. Murphy and A.A. D'Addieco. 1945. Chlorite holocellulose, its fractionation and bearing on summative wood analysis and on studies on the hemicelluloses. *Section of the Technical Association of the Pulp and Paper Industry*, 122:11–19.
- Yang, S. and M.T. Tyree. 1994. Hydraulic architecture of *Acer saccharum* and *A. rubrum*: comparison of branches to whole trees and the contribution of leaves to hydraulic resistance. *J. Exp. Bot.* 45: 179–186.
- Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, New York, 139 p.