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Canopy and hydraulic conductance in young, mature and old Douglas-fir trees

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Summary We tested for reductions in water transport with increasing tree size, a key component in determining whether gas exchange and growth are hydraulically limited in tall trees. During the summers of 1998 and 1999, we measured water transport with Granier-type, constant-heat sap flow probes, vapor pressure deficit, and leaf and soil water potentials in overstory *Pseudotsuga menziesii* (Mirb.) Franco trees in three stands differing in size and age (15, 32 and 60 m in height and about 20, 40 and 450 years in age, respectively) in a *P. menziesii*-dominated forest in the Pacific Northwest, USA. A total of 24 trees were equipped with sap flow sensors—six 60-m trees, nine 32-m trees and nine 15-m trees. Based on the sap flow measurements and leaf area information estimated from leaf area–sapwood area relationships, we estimated crown-averaged stomatal conductance (G_S) and leaf-specific hydraulic conductance (K_L). We tested the hypothesis that G_S and K_L vary inversely with tree height (15 > 32 > 60 m). Analysis of variance of G_S ranked as 15 = 60 > 32 m during the early summer and 15 > 60 > 32 m during late season drought. Over the growing season, mean daily G_S (± SE) was 29.2 ± 4.4, 24.0 ± 6.8 and 17.7 ± 7.2 mmol m^{-2} s^{-1} for the 15-, 60- and 32-m trees, respectively. The value of K_L differed among tree heights only during late season drought and ranked 15 > 32 = 60 m. A hydraulic mass balance suggests that greater sapwood conductivity in 60-m trees compared with 32- and 15-m trees is a likely cause for the departure of the above rankings from those predicted by height and leaf-to-sapwood area ratio.

Keywords: forest age, hydraulic limitation, Pseudotsuga menziesii, sap flux, xylem.

Introduction

Several studies have found substantial reductions in stomatal or crown conductance to gas exchange with increasing tree size and age (Yoder et al. 1994, Hubbard et al. 1999, Ryan et al. 2000, Shäfer et al. 2000). Reductions in stomatal or crown conductance were shown to be associated with increased hydraulic resistance (Yoder et al. 1994, Hubbard et al. 1999). Whole-tree estimates of leaf-specific hydraulic conductance were also lower in larger, older trees than in smaller, younger trees in several species (Mencuccini and Grace 1996, Ryan et al. 2000). These studies support the hydraulic limitation hypothesis, which states that tree height growth and productivity decline because of stomatal limitation induced by increased hydraulic path-length resistance and gravity (Ryan and Yoder 1997). For such hydraulic limitation to occur, taller trees must show both (1) reduced leaf-specific hydraulic conductance and (2) reduced crown stomatal conductance compared with smaller trees of the same species growing in similar site conditions. In this study, we tested for reduced leaf-specific hydraulic conductance and crown-averaged stomatal conductance with increasing tree height in *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir).

In 1998, we installed instruments for estimating crown gas-phase conductance in an old Douglas-fir–western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest (60 m tall, 450 years old) and two nearby younger sites: a 32-m stand established in 1958 and a 15-m stand established in 1977. Mean annual height growth of trees in these stands was 6, 93 and 96 cm, respectively. Stemwood growth efficiency averaged 27.9, 34.7 and 59.8 g C m^{-2} leaf area $year^{-1}$ for the 60-, 32- and 15-m trees, respectively (N.G. McDowell, unpublished data). Here we report results comparing crown-averaged stomatal conductance (G_S) and whole-tree leaf-specific hydraulic conductance (K_L) in dominant Douglas-fir individuals at the three sites. We tested the hypothesis that G_S and K_L decrease with increasing tree height.

Materials and methods

Sites and species

The three study sites were located within 10 km of each other

in the Wind River Basin in southern Washington, USA. Details of the sites are provided in Table 1. The site with the 60-m high trees (hereafter 60-m site) was located at the Wind River Canopy Crane Research Facility (45°49′13.76″ N, 121°57′06.88″ W) at an elevation of 368 m. The sites with the 15- and 32-m high trees (hereafter 15- and 30-m sites) were located at 45°49′07.89″ N, 121°59′38.95″ W, elevation of 558 m and 45°49′16.21″ N, 122°1′50.55″ W, elevation of 582 m, respectively. Mean annual precipitation in this region is 2.5 m, over 70% of which falls as snow, with a dry season from June through September. Mean annual temperature is 8.7 °C. Soils in the region are well drained and of volcanic origin.

Instrumentation and sampling

Constant-heat sap flow sensors (Granier 1985, 1987) were installed in six dominant trees at the 60-m site and nine dominant trees at each of the 32- and 15-m sites. Sap flow data from these sensors were collected during June–September 1998 and 1999 at the 60- and 15-m sites, and during June–September 1999 at the 32-m site. Table 1 contains information about the trees used for sap flow measurements. All six trees at the 60-m site were equipped with three 20-mm-long sensors inserted 0–20 mm inside the cambium and spaced evenly around the circumference of each tree at 3–4 m above ground. All nine trees at each of the 32- and 15-m sites were equipped with two 20-mm-long sensors on opposite sides of the tree approximately 3 and 2 m above ground, respectively. In 1998, three of the six trees at the 60-m site and five of the nine trees at the 15-m site were equipped with 30-mm-long sensors. Sapwood depth measurements, visually inspected from increment cores, indicated that none of the sensors crossed the heartwood boundary.

In 1999, representative trees (two trees in the 60-m stand and three trees each in the 32- and 15-m stands) were used to account for radial profiles in sap flux density (Phillips et al. 1996). In the 60-m trees, two 20-mm sensors were inserted 15–35 mm inside the cambium. In the 32- and 15-m trees, a 20-mm sensor was inserted 15–35 mm inside the cambium. Radial profiles from 1999 were used in the scaling of whole-tree fluxes for both 1998 and 1999.

Temperature differences from all pairs of probes were converted to sap flux density (J_S, g H_2O m^{-2} sapwood s^{-1}) based on an empirical equation developed by Granier (1987) that included Douglas-fir in the data set. Sap flux in the inner 15–35 mm of trees ($J_{S,in}$) that were not equipped with inner sap flow probes was estimated from a relationship between $J_{S,in}/J_{S,out}$ and diameter at 1.3 m height (diameter at breast height; DBH), where $J_{S,out}$ is sap flux density in the outer 0–20 mm zone. Very little sapwood extended to a depth beyond 35 mm (Table 1), but any such sapwood was assumed to have the same flux rate as $J_{S,in}$. Sap flow rates on a whole-tree basis (J) were computed as the weighted average of sap flow in inner and outer zones.

Predawn soil water potential (Ψ_S) was measured periodically throughout the summers of 1998 and 1999 by treating western hemlocks at each site as soil tensiometers during predawn conditions and sampling leaf water potential (Ψ_l) from their crowns, under the assumption that Ψ_l of the western hemlocks (~5 m in height) had equilibrated with bulk Ψ_S by predawn. The validity of this approach is supported by findings that predawn water potential gradients in large Douglas-fir trees at Wind River approached the theoretical hydrostatic gradient (Bauerle et al. 1999). Also, we noted that dew point was observed throughout the season during sampling periods, and thus the likelihood of nighttime water loss by western hemlock needles was minimal. Volumetric soil water content (θ; m^3 m^{-3}) was estimated on a semi-weekly basis by time-domain reflectometry (Nikodem 1966, Topp and Davis 1985), with pairs of stainless steel rods 1 m in length installed vertically in five locations in each of the sites. To estimate θ, we used regressions developed at each site relating θ to the time interval between the reflection of an electromagnetic pulse from the soil surface to the rod ends.

Air temperature and relative humidity were measured in the upper third of the canopy of trees at the 60-m site with a Vaisala HMP35C Temperature/Humidity Probe (Campbell Scientific, Logan, UT). These data were obtained from the meteorological database of the Wind River Canopy Crane Research Facility. At the 32- and 15-m sites, air temperature and relative humidity were measured in the upper third of the canopy of the trees with CS500 temperature and relative humidity probes (Campbell Scientific). Photosynthetically active radiation (Q_o) was measured with a Li-Cor 190SA quantum sensor (Li-Cor, Lincoln, NE) above the canopy at the 60-m site. All

Table 1. Site and tree characteristics. Numbers in brackets are standard errors. Abbreviation: LAI = leaf area index.

Height (m)	Age (years)	Density (> 5 cm DBH) (trees ha^{-1})	Plot LAI	Douglas-fir LAI	Basal area (% Douglas-fir) (m^2 ha^{-1})	Sapwood area[1] (m^2 ha^{-1})	A_L:A_S[2] (m^2 cm^{-2})	Sap flow trees diameter (m)	Sapwood depth (cm)
15	20	3057	11(6)[3]	11(6)[3]	46.9 (97%)	23.9	0.51 (0.051)	0.18 (0.034)	3.5 (0.6)
32	40	1420	8	6	38.4 (68%)	12.7	0.49 (0.065)	0.38 (0.066)	3.9 (0.6)
60	450	448[2]	9	2	35.6[4] (43%)	4.51	0.39 (0.078)	1.05 (0.26)	4.1 (1.2)

[1] Douglas-fir only.
[2] Estimate from N.G. McDowell (unpublished data).
[3] The LAI of 11 at the 15-m site is the average LAI from two 15 × 15-m plots immediately surrounding the sap flow trees in 1998 and 1999. The LAI of 6 for this site is from a survey conducted in July 2000 of the entire clear-cut, which contains many areas of poor regeneration.
[4] Data from Wind River Canopy Crane Research Facility Web Page (http://depts.washington.edu/wrccrf/database.html).

sap flow and meteorological data were sampled at 10-s intervals, and averaged and recorded at 30-min intervals.

Scaling

Sap flux per unit sapwood area was scaled to a unit leaf area basis (E) in each plot as:

$$E = \frac{\bar{J}}{A_L{:}A_S}, \quad (1)$$

where $A_L{:}A_S$ is the leaf-to-sapwood area ratio, obtained for each tree age/size class in a separate study (N.G. McDowell, unpublished data).

Crown-averaged stomatal conductance (G_S) was estimated every half hour as:

$$G_S = \frac{\bar{E}D}{P}, \quad (2)$$

where P is atmospheric pressure and D is vapor pressure deficit, assumed to be close to the foliage-to-air vapor pressure difference. This assumption is generally valid in conifer forests (Jarvis and McNaughton 1986) unless wind speeds are very low (Martin et al. 1999). No lag between instantaneous E and D was applied because the correlation was maximum at zero lag at all three sites ($r^2 = 0.85$, 0.79 and 0.78 for the mean values for 15-, 32- and 60-m trees, respectively). A simple lag generally cannot fully account for the use of stored water in trees caused by the interaction of hydraulic resistance and capacitance (Phillips and Oren 1998). Therefore, we also computed a daily averaged canopy conductance (hereafter referred to as daily G_S) that averages D and E on a daily time step, and then used these daily variables to compute conductance (Phillips and Oren 1998).

Whole-tree leaf-specific hydraulic conductance was computed as:

$$K_L = \frac{E}{\Psi_l - \Psi_S - \rho g h}, \quad (3)$$

where ρ is the density of liquid water, g is the acceleration due to gravity and h is canopy height (assumed to be 15, 32 and 60 m at the appropriate sites). In Equation 3, we used mean values of E and Ψ_l calculated for the period 1000–1500 h. Thus, K_L is a relatively coarse-scale daily estimate, but is less subject to errors introduced by temporal decoupling between sap flow derived E and Ψ_l. Error estimates and error propagation for the above estimates are discussed in the Appendix.

Results

Diurnal transpiration and canopy conductance

Overall differences in half-hourly G_S and E among the three size classes were highly significant (ANOVA, $P < 0.0001$ for daylight hours, defined as between 1000 and 2000 h). However, the ranking of sites was not in the order hypothesized, and the rankings showed a dependency on the period in the growing season. The most striking result was that, among size classes, half-hourly G_S and E in the 32-m trees were consistently the lowest, as shown in monthly means of diurnal time series (Figure 1). Half-hourly G_S and E declined in the 60-m trees compared with the 15-m trees in the late summer of both 1998 and 1999 (Figures 1 and 2). When data were averaged over the entire collection period for conditions of ample light ($Q_o > 700$ μmol m^{-2} s^{-1}) and moderate D (0.75 kPa < D < 1.25 kPa), half-hourly G_S ranked as 15 = 60 > 32 m (least significant difference (LSD), $P < 0.0001$).

Daily canopy conductance

Daily G_S ranked as 15 = 60 > 32 m (LSD $P = 0.04$) during the months of June, July and August, but it ranked as 15 > 60 > 32 m (LSD $P < 0.05$ for all contrasts) in September. Mean daily G_S (± SE) was 29.2 ± 4.4, 17.7 ± 7.2 and 24.0 ± 6.8 mmol m^{-2} s^{-1} for the 15-, 32- and 60-m trees, respectively. These values are lower than the mean values of leaf-level stomatal conductance (60 mmol m^{-2} s^{-1}) found by Tan and Black (1976) in a 10-m tall Douglas-fir plantation.

Leaf-specific hydraulic conductance

Although K_L did not differ among sites in the early growing season ($P > 0.1$), in the late season it ranked 15 > 60 = 32 m (LSD $P < 0.0001$; September 1999; Figure 4). The limited data for K_L in 1998 were consistent with K_L values for comparable periods in 1999 (cf. Figures 3a and 3b). The mean values of K_L reported here (about 0.2–0.5 mmol m^{-2} s^{-1} MPa^{-1}) are somewhat less than the values of about 0.5–0.6 mmol m^{-2} s^{-1} MPa^{-1} reported by Whitehead and Jarvis (1981) (from data in Nnyamah et al. (1978)) for a 7–10-m tall Douglas-fir forest, and less than the value of 1.1 mmol m^{-2} s^{-1} MPa^{-1} reported for 22–27-year-old Douglas-fir trees by Bond and Kavanagh (1999), which was based on transpiration of 1-year-old foliage in the upper crowns. We note that K_L is a measure of conductance within plants and does not incorporate the effect of gravity, which varies considerably among these size classes. To better compare the combined effects of plant and gravitational resistance, we also computed an adjusted K_L that accounts for gravitational differences (i.e., we eliminated the $-\rho g h$ term in the denominator of Equation 3). Gravitational differences did not alter the statistical rankings for the adjusted K_L from the K_L presented above.

Size-related differences in radial patterns of sap flow

We found size-dependent variation in the radial pattern of flux. Averaged over the summer months of 1999, the ratio of J_S in the 15–35 mm sapwood band inside the cambium to that in the 0–20 mm sapwood band in relation to DBH showed an exponential saturation of the form: $J_{S,in}/J_{S,out} = 1.27(1 - e^{-2.44DBH(m)})$ ($r^2 = 0.73$; $P = 0.0066$, $n = 8$ trees; Figure 4). Over the June–September 1999 period, sap flow in the inner part of the sapwood decreased substantially relative to outer sap flow in the smaller trees, but less so in the large trees (Figure 5).

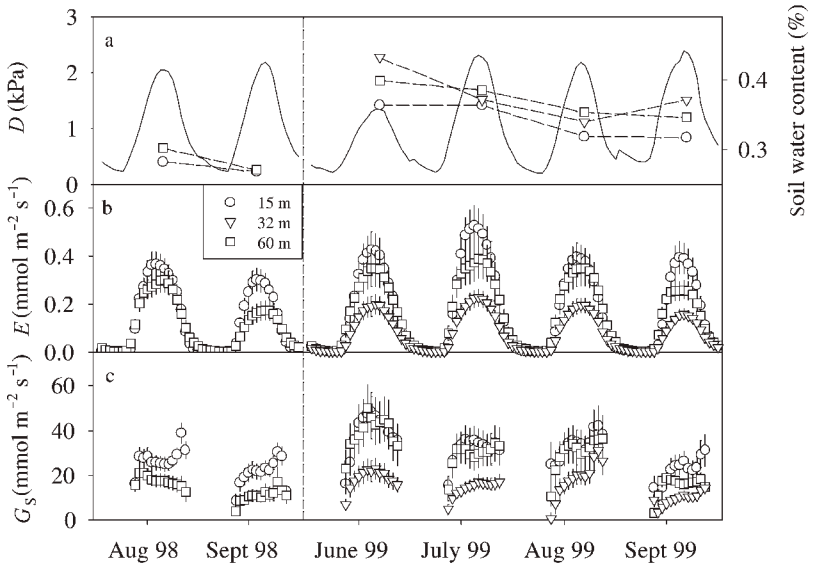

Figure 1. (a) Diurnal time series of vapor pressure deficit (D) from the 60-m site and mean monthly water contents at the 15-m (○), 32-m (▽) and 60-m (□) sites. Each value of D is averaged from half-hourly values within a month. (b) Diurnal time series of water flux per unit leaf area (E) for the 15-, 32- and 60-m trees. Symbols and time averaging are as in Panel (a). Standard error bars are from the variation among trees. (c) Crown-averaged stomatal conductance (G_S) for the 15-, 32- and 60-m trees. Symbols, time averaging and standard error bars are as in Panel (b).

Within diurnal periods, the relationship between inner and outer sap flux appeared to be linear in all trees. Averaging within size classes, and splitting the total data set into early and late season halves, the slope of the linear relationship between inner and outer sap flow decreased from 0.59 ($r^2 = 0.93$) to 0.31 ($r^2 = 0.87$) in 15-m trees, from 0.60 ($r^2 = 0.91$) to 0.41 ($r^2 = 0.87$) in 32-m trees, and from 0.79 ($r^2 = 0.96$) to 0.74 ($r^2 = 0.99$) in 60-m trees.

Soil and leaf water status

Soil water content was lowest during the late summer of 1998 at the same time that vapor pressure deficit was high (Figure 1a). The largest reductions in half-hourly G_S and E of 60-m trees compared with 15-m trees occurred during this period (Figures 1b, 1c and 2). Monthly means of Ψ_S estimated from predawn Ψ_l of small trees were similar among sites except for a reduced Ψ_S at the 15-m site toward the late season in 1999 (Figure 6a). During both years, Ψ_S remained between –0.5 and –1.1 MPa at the 15-m site and between –0.5 and –0.7 MPa at the 32- and 60-m sites, respectively (Figure 6a). Mean monthly midday Ψ_l was consistently lowest in the 60-m trees, approaching –3.0 MPa in the late season of 1999, whereas mean monthly midday Ψ_l values of 15- and 32-m trees were in the range of –1.5 to –2.0 MPa (Figure 6b).

Discussion

The hypothesis that canopy conductance and leaf-specific hydraulic conductance vary simply as the inverse of tree height was not supported by our results. Among the trees studied, the 32-m trees consistently showed the lowest G_S, and K_L of the 32-m trees was not significantly different from that of the 60-m trees. However, the effect of low soil water content on G_S and K_L was most pronounced for the 60-m trees, suggesting some differential influence of soil water limitation with tree height.

Our study suggests that the structural change in the aboveground portions of the trees may moderate the influence

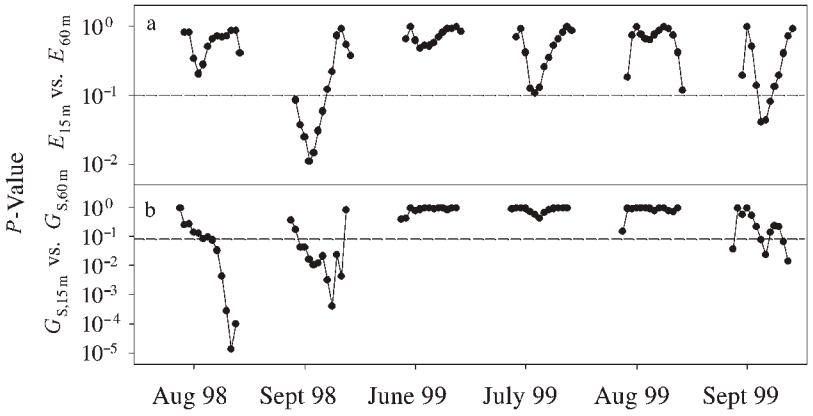

Figure 2. P-Values for the differences in (a) half-hourly water flux per unit leaf area (E) and (b) half-hourly crown-averaged stomatal conductance (G_S), from the data shown in Figure 1. Contrasts with 32-m trees are not shown because they were always significantly different ($P < 0.0001$) from both 15- and 60-m trees.

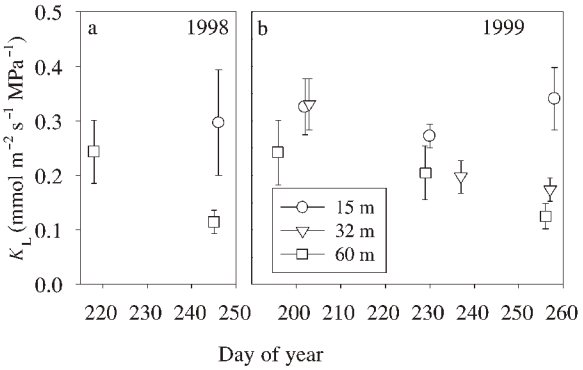

Figure 3. Leaf-specific tree hydraulic conductance, K_L (mmol m^{-2} s^{-1} MPa^{-1}) in (a) 1998 and (b) 1999, in 15-m trees (○), 32-m trees (▽) and 60-m trees (□). Bars represent one standard error.

of size on K_L and G_S. The A_L:A_S ratio was about 25% lower in 60-m trees (0.39 m^2 cm^{-2}) than in 32-m (0.49 m^2 cm^{-2}) and 15-m trees (0.51 m^2 cm^{-2}) (N. G. McDowell, unpublished data). The decrease in A_L:A_S in the 60-m trees may have increased the redundancy of the water conducting system to foliage and perhaps provided a source of stored water for short-term gas exchange.

Could the variation in A_L:A_S alone account for the rankings of G_S in this study? A simple mass balance model employed by Shäfer et al. (2000) was used to answer this question. Under steady-state conditions and uniform D, the ratio of G_S in trees of different heights can be expressed as:

$$\frac{G_{S1}}{G_{S2}} = \frac{k_{s1}}{k_{s2}} \frac{A_{L2}:A_{S2}}{A_{L1}:A_{S1}} \frac{h_2}{h_1} \frac{\Delta\Psi_{S-L,1} - 0.01h_1}{\Delta\Psi_{S-L,2} - 0.01h_2}, \quad (4)$$

where the numerical subscripts refer to trees of different heights, k_s is specific conductivity of sapwood, h is mid-canopy height (m) and $\Delta\Psi_{S-L}$ is the soil to leaf water potential difference. Based on the values of A_L:A_S, h and $\Delta\Psi_{S-L}$, and

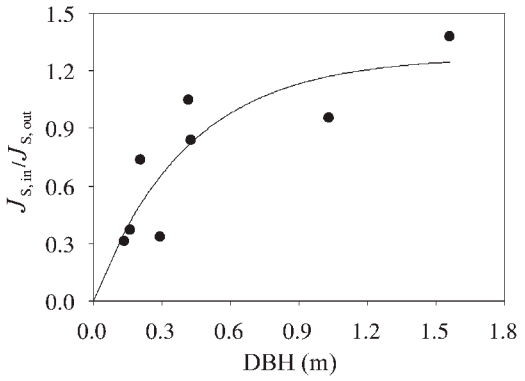

Figure 4. Relationship between inner sap flux ($J_{S,in}$; 15–35 mm beneath cambium) to outer sap flux ($J_{S,out}$; 0–20 mm beneath cambium) ratio and tree diameter at 1.3 m height (DBH).

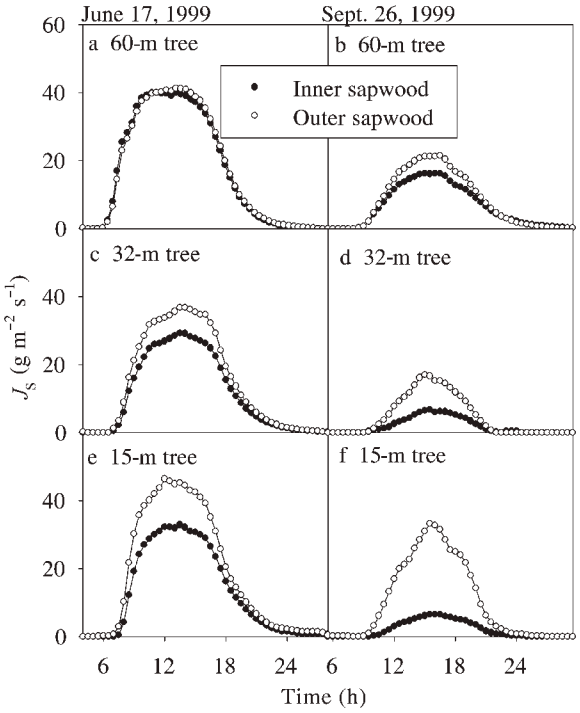

Figure 5. Representative early (June 17, 1999; a, c, e) and late (September 26, 1999; b, d, f) season diurnal courses of outer (0–20 mm beneath cambium; ○) and inner (15–35 mm; ●) sap flux density (J_s) in a 60-m tree (a, b), 32-m tree (c, d) and 15-m tree (e, f).

assuming that mean k_s does not change with tree size, the G_S ratio of 15- to 32-m trees is predicted to be 1.8, which is reasonably close to the mean ratio of 2.0 from the results of this study. However, the G_S ratio of 15- to 60-m trees is predicted to be 1.9, whereas we found the mean ratio to be 1.1. This sug-

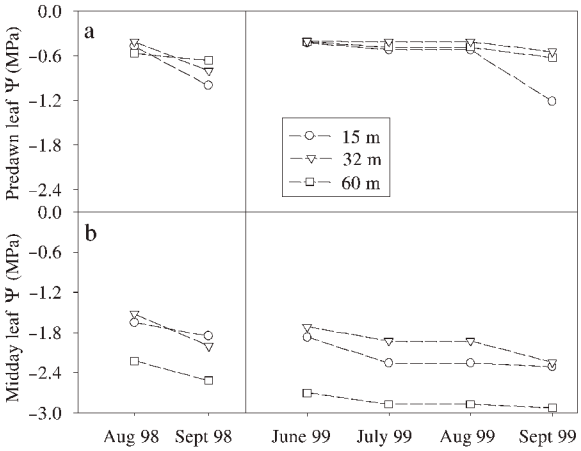

Figure 6. Mean monthly (a) soil water potential, estimated from predawn leaf water potential of small trees, and (b) midday leaf water potential of 15-m (○), 32-m (▽) and 60-m (□) trees.

gests that the assumption of uniform k_s with tree size may be adequate when comparing 15- and 32-m trees but not when comparing 15- or 32-m trees with 60-m trees. More specifically, this model suggests that k_s in 60-m trees is almost twice that in 15-m trees. Such a large change in k_s seems unlikely and may indicate the limitations of this simple model, but nevertheless raises the question of whether increases in sapwood conductivity may compensate for increased path length resistance. There is previous evidence for increases in sapwood permeability with tree size (Pothier et al. 1989).

In addition to possible alterations in structural or anatomical traits with tree size, we cannot ignore the possibility of inherent site differences that may have influenced our results. For example, the 32-m site has higher soil and leaf nitrogen than the 15- or 60-m sites (Klopatek 2002, N. G. McDowell, unpublished data). Increased soil fertility may lead to a decrease in root allocation relative to foliage (Oren and Sheriff 1995). It is possible that a lower root surface area could generate a high root resistance at the onset of transpiration, thus inducing the lower observed E and G_S. Our measurements would not be able to account for such a site fertility effect.

To the extent that crown conductance controls carbon uptake and tree height growth, the rankings of G_S and K_L found here do not appear to be consistent with the observed annual height growth of the trees (6, 93 and 96 cm, in the 60-, 32- and 15-m trees, respectively). Yet in terms of annual accumulation of aboveground biomass per unit leaf area (growth efficiency), the 32-m trees were more similar to the 60-m trees than to the 15-m trees (27.9, 34.7 and 59.8 g C m^{-2} leaf area $year^{-1}$ for the 60-, 32- and 15-m trees, respectively). Clearly, different mechanisms control height versus biomass increment in a given year, and annual height growth is not necessarily the best correlate with leaf or crown gas exchange. In particular, our K_L results, especially during the late season (Figure 3), are more consistent with rankings of aboveground productivity, relative to leaf area, than they are with absolute tree height.

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References

Bauerle, W.L., T.M. Hinckley, J. Čermák, J. Kucera and K. Bible. 1999. The canopy water relations of old-growth Douglas-fir trees. Trees 13:211–217.

Bond, B.J. and K.L. Kavanagh. 1999. Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. Tree Physiol. 19:503–510.

Clifford, A.A. 1973. Multivariate error analysis: A handbook of error propagation and calculation in many-parameter systems. John Wiley, New York, 112 p.

Granier, A. 1985. Une nouvelle méthode pour la mesure de flux de sève brute dans le tronc des arbres. Ann. Sci. For. 42:193–200.

Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol. 3:309–320.

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.

Jarvis, P.G. and K.G. McNaughton. 1986. Stomatal control of transpiration: scaling up from leaf to region. Adv. Ecol. Res. 15:1–49.

Klopatek, J.M. 2002. Belowground carbon pools and processes in different age stands of Douglas-fir. Tree Physiol. 22:197–204.

Martin, T.A., T.M. Hinckley, F.C. Meinzer and D.G. Sprugel. 1999. Boundary layer conductance, leaf temperature and transpiration of *Abies amabilis* branches. Tree Physiol. 19:435–443.

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.

Nikodem, H.J. 1966. Effects of soil layering on the use of VHF radio waves for remote terrain analysis. Proc. 4th Symp. Remote Sensing Environ., Univ. Michigan, Ann Arbor, pp 691–703.

Nnyamah, J.U., T.A. Black and C.S. Tan. 1978. Resistance to water uptake in a Douglas-fir forest. Soil Sci. 126:63–76.

Oren, R. and D.W. Sheriff. 1995. Water and nutrient acquisition by roots and canopies. *In* Resource Physiology of Conifers. Eds. W.K. Smith and T.M. Hinckley. Academic Press, San Diego, 396 p.

Oren, R., N. Phillips, G.G. Katul, B.E. Ewers and D.E. Pataki. 1998. Scaling xylem sap flux and soil water balance and calculating variance: a method for partitioning water flux in forests. Ann. Sci. For. 55:191–216.

Phillips, N. and R. Oren. 1998. A comparison of daily representations of canopy conductance based on two conditional time-averaging methods and the dependence of daily conductance on environmental factors. Ann. Sci. For. 55:217–235.

Phillips, N., R. Oren and R. Zimmermann. 1996. Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. Plant Cell Environ. 19:983–990.

Pothier, D., H.A. Margolis and R.H. Waring. 1989. Patterns of change of saturated sapwood permeability and sapwood conductance with stand development. Can. J. For. Res. 19:432–439.

Ryan, M.G. and B.J. Yoder. 1997. Hydraulic limits to tree height and tree growth. Bioscience 47:235–242.

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.

Shäfer, K.V.R., R. Oren and J.D. Tenhunen. 2000. The effect of tree height on crown level stomatal conductance. Plant Cell Environ. 23:365–375.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd Edn. W.H. Freeman and Company, New York, 859 p.

Tan, C.S. and T.A. Black. 1976. Factors affecting the canopy resistance of a Douglas-fir forest. Boundary Layer Meteorol. 10: 475–488.

Taylor, J.R. 1982. An introduction to error analysis: The study of uncertainties in physical measurements. Oxford University Press, Mill Valley, CA, 270 p.

Topp, G.C. and J.L. Davis. 1985. Measurement of soil water content using time domain reflectometry (TDR): a field evaluation. Soil Sci. Soc. Am. J. 49:19–24.

Whitehead, D. and P.G. Jarvis. 1981. Coniferous forests and plantations. *In* Water Deficits and Plant Growth. Vol. VI. Woody Plant Communities. Ed. T.T. Kozlowski. Academic Press, New York, pp 50–132.

Yoder, B.J., M.G. Ryan, R.H. Waring, A.W. Schoettle and M.R. Kaufmann. 1994. Evidence of reduced photosynthetic rates in old trees. For. Sci. 40:513–527.

Zar, J.H. 1984. Biostatistical analysis. 2nd Edn. Prentice Hall, Englewood Cliffs, NJ, 718 p.

Appendix

Error estimates

Variance estimates for J were computed as the sample variance:

$$\sigma_J^2 = \frac{\sum (J_i - \bar{J})^2}{n-1}. \quad \text{(A1)}$$

Similar to the approach taken by Oren et al. (1998), variance estimates for E were computed according to Taylor (1982, p 177) and Clifford (1973, p 34), to include the effects of error in both J and A_L:A_S and their possible mutual dependency as:

$$\sigma_E^2 = \left(\frac{\partial E}{\partial J}\right)\sigma_J^2 + \left(\frac{\partial E}{\partial A_L{:}A_S}\right)\sigma_{A_L:A_S}^2 + 2\left(\frac{\partial E}{\partial J}\frac{\partial E}{\partial A_L{:}A_S}\right)\sigma_J\,\sigma_{A_L:A_S}\,r(J, A_L{:}A_S), \quad \text{(A2)}$$

where σ denotes a standard deviation, $r(J, A_L{:}A_S)$ is the correlation coefficient between J and A_L:A_S, and $\partial E/\partial J = 1/A_L{:}A_S$ and $\partial E/\partial A_L{:}A_S = -J/(A_L{:}A_S)^2$ from Equation 1. The quantities $\sigma_{A_L:A_S}$ for each site are from N. G. McDowell (unpublished data) and are shown in Table 1.

Similarly, variance estimates for half-hourly and daily G_S were computed as:

$$\sigma_{G_S}^2 = \left(\frac{\partial G_S}{\partial E}\right)\sigma_E^2 + \left(\frac{\partial G_S}{\partial D}\right)\sigma_D^2 + 2\left(\frac{\partial G_S}{\partial E}\frac{\partial G_S}{\partial D}\right)\sigma_E\,\sigma_D\,r(E, D), \quad \text{(A3)}$$

where σ_E^2 is taken from Equation A2 and $r(E,D)$ is the correlation coefficient between E and D. For σ_D^2 we used accuracy information from the CS500 and HMP35C specifications provided in the Instruction Manuals by Campbell Scientific and estimated that $\sigma_D = 0.0065T(°C) - 0.00055RH(\%)$ ($r^2 = 0.96$; $P < 0.0001$). For example, at $T = 25$ °C and RH = 50%, $D = 1.58$ kPa and $\sigma_D = 0.14$ kPa. Variance estimates for K_L were also computed as above using σ_E^2 from Equation 8 and mean variance of Ψ_l over the period from 1000 to 1500 h.

Analysis of variance (ANOVA) was performed to test for between-site differences in half-hourly and daily G_S and K_L. We computed the ANOVA using means and variances given in Zar (1984, p 168). This approach allowed us to include in the ANOVA full variance estimates for E, G_S and K_L as given in Equations A2 and A3, which cannot be obtained from individual estimates of E, G_S and K_L (because those quantities are functions of mean A_L:A_S, not individual A_L:A_S, and therefore are not sampled individually). If a posteriori results showed that any two sites were not different in G_S or K_L, contrasts of those sites against the third were employed using the least significant difference method (Sokal and Rohlf 1981, pp 242–244).

To compute variance in estimates of half-hourly or daily E and G_S, correlation coefficients between J and A_L:A_S were necessary. From subsets of trees sampled for both J and A_L:A_S, there were no relationships between J and A_L:A_S at the 15-m site ($P = 0.6$, $n = 4$), or at the 32-m site ($P = 0.11$, $n = 6$). The A_L:A_S ratio at the 60-m site was not sampled from the same individuals as was J (because of sampling restrictions at the Wind River Canopy Crane Research Facility), so it was not possible to check for a relationship between J and A_L:A_S in the 60-m trees. However, when mean J and mean A_L:A_S from the 60-m site were combined with individual J and A_L:A_S from both the 15-m site and the 32-m site, no relationship was found ($P = 0.9$, $n = 11$). Therefore, we used $r(J, A_L{:}A_S) = 0$ in computing σ_E^2 (Equation A2).

To compute variance in estimates of half-hourly or daily G_S in Equation A3, correlation coefficients between E and D at each site were necessary. The relationships between mean daily E and mean daily D were best described by exponential saturation curves rather than linear functions. While the correlation coefficient used in Equation A3 is for a linear relationship, we assumed that the correlation coefficients for the saturating exponential relationships could be used. These values were $r = 0.70$, 0.70 and 0.51 for the 15-, 32- and 60-m sites, respectively. All three of these relationships were highly significant ($P < 0.0001$).