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An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees

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Summary The hydraulic limitation hypothesis (Ryan and Yoder 1997) proposes that leaf-specific hydraulic conductance (k_l) and stomatal conductance (g_s) decline as trees grow taller, resulting in decreased carbon assimilation. We tested the hydraulic limitation hypothesis by comparison of canopy-dominant Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) trees in stands that were approximately 15 m (20 years old), 32 m (40 years old) and 60 m (> 450 years old) tall in Wind River, Washington, USA. Carbon isotope discrimination (Δ) declined with tree height (18.6, 17.6 and 15.9‰ for stands 15, 32 and 60 m tall, respectively) indicating that g_s may have declined proportionally with tree height in the spring months, when carbon used in the construction of new foliage is assimilated. Hydraulic conductance decreased by 44% as tree height increased from 15 to > 32 m, and showed a further decline of 6% with increasing height. The general nonlinear pattern of k_l versus height was predicted by a model based on Darcy's Law. Stemwood growth efficiency also declined nonlinearly with height (60, 35 and 28 g C m^{-2} leaf area for the 15-, 32- and 60-m stands, respectively). Unlike k_l and growth efficiency, g_s and photosynthesis (A) during summer drought did not decrease with height. The lack of decline in cuvette-based A indicates that reduced A, at least during summer months, is not responsible for the decline in growth efficiency. The difference between the trend in g_s and A and that in k_l and Δ may indicate temporal changes (spring versus summer) in the response of gas exchange to height-related changes in k_l, or it may be a result of measurement inadequacies. The formal hydraulic limitation hypothesis was not supported by our mid-summer g_s and A data. Future tests of the hydraulic limitation hypothesis in this forest should be conducted in the spring months, when carbon uptake is greatest.

We used a model based on Darcy's Law to quantify the extent to which compensating mechanisms buffer hydraulic limitations to gas exchange. Sensitivity analyses indicated that without the observed increases in the soil-to-leaf water potential differential ($\Delta\Psi$) and decreases in the leaf area/sapwood area ratio, k_l would have been reduced by more than 70% in the 60-m trees compared with the 15-m trees, instead of the observed decrease of 44%. However, compensation may have a cost; for example, the greater $\Delta\Psi$ of the largest trees was associated with smaller tracheid diameters and increased sapwood cavitation, which may have a negative feedback on k_l and g_s.

Keywords: age-related growth decline, carbon isotope discrimination, hydraulic conductance, old trees, Pseudotsuga menziesii, stomatal conductance.

Introduction

A size- or age-related reduction in leaf-specific hydraulic conductance (k_l) has been suggested as a mechanism that constrains stomatal conductance (g_s) of tall trees, causing reduced photosynthesis (A) and subsequent reductions in primary productivity (Yoder et al. 1994). Leaf-specific hydraulic conductance may decrease with tree size as a result of a greater path length from soil to stomata, increased sapwood density, and the gravitational pull on water columns of large trees. Stomatal conductance is expected to decline proportionally with reduced k_l because of the fundamental interdependence of these two variables (Sperry et al. 1993, Hubbard et al. 2001). Reductions in g_s will reduce leaf conductance to CO_2, causing A and, in turn, annual gross primary production to decline (Gower et al. 1996, Ryan et al. 1997). This theory was formalized as the "hydraulic limitation hypothesis" (Ryan and Yoder 1997), which requires that the tenets described above be met before age-related growth decline can be attributed to hydraulic limitation. Specifically, these tenets are: (1) k_l must decrease with increasing tree size; (2) g_s and A must decrease concurrently with decreasing k_l; and (3) the reduction in A must be sufficient to account for reduced growth (Ryan and Yoder 1997).

However, increases in size may provide a driving force for physiological and structural changes that act to minimize size-related constraints on leaf-specific gas exchange. These "com-

pensation" mechanisms could increase the water transport capacity of the tree relative to the total leaf area (Ryan and Yoder 1997, Becker et al. 2000). Potential changes include, but are not limited to: (1) increased sapwood specific conductivity (Pothier et al. 1989); (2) increased sapwood area relative to leaf area (McDowell et al. 2002); (3) an increased driving force for water transport (the water potential difference between soil and leaf; Hacke et al. 2000); (4) increased root surface area (Sperry et al. 1998, Magnani et al. 2000); and (5) increased water storage (Waring and Running 1978, Goldstein et al. 1998, Phillips et al. 2002). There is further evidence for the above-mentioned changes from both theoretical and experimental analyses (Becker et al. 2000, Bond and Ryan 2000, Mencuccini and Magnani 2000).

The objective of our study was to test the hydraulic limitation hypothesis and examine potential compensation for hydraulic limitations in three age and size classes of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) located at the Wind River Experimental Forest in southwestern Washington, USA.

Theory

Hydraulic limitation

Leaf-specific hydraulic conductance can be expressed as:

$$k_l = \frac{E_l}{\Psi_{soil} - \rho g h - \Psi_{leaf}}, \quad (1)$$

where E_l is vapor-phase water flux (transpiration), Ψ_{leaf} and Ψ_{soil} are leaf and soil water potential, respectively, and $\rho g h$ is the effect of gravity (g is the acceleration due to gravity) at a given height (h) and water density (ρ) (symbols and units are provided in Table 1). This expression of hydraulic conductance does not include the effect of height; that is, it is equivalent to the conductance of a stem lying horizontally on the ground. Vapor-phase water flux equals liquid-phase water flux when water storage is zero (i.e., steady-state), such as during midday (Phillips et al. 2002). Stomatal conductance is related to k_l because the following expression can replace E_l in Equation 1:

$$E_l = g_s D, \quad (2)$$

where D is vapor pressure deficit from leaf to air. Equation 2 is valid if leaves are well coupled to the atmosphere. From Equations 1 and 2, we predict that if k_l declines as a result of increases in path length or tortuosity, or for other reasons, then g_s should decline proportionally. This direct relationship between k_l and g_s assumes that D is constant and that midday minimum Ψ_{leaf} does not change with tree height, which has been found for ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws & C. Laws), but not for lodgepole pine (*P. contorta* var. *latifolia* Engelm. ex S. Wats.) (Yoder et al. 1994). Assuming no change in Ψ_{leaf} or D, then from Equations 1 and 2 we see that a decline in k_l will result in a proportional decline in g_s (Ryan and Yoder 1997).

Examination of three tree height classes provided us with the opportunity to test the prediction that height would be inversely proportional to k_l (Mencuccini and Grace 1996*a*). The specific relationship between height and k_l has been found to be nonlinear, with a steep initial drop in k_l as height increases, leading to a plateau in which k_l becomes nearly constant with any further increases in height (Mencuccini and Grace 1996*a*). This pattern is predicted by a hydraulic corollary of Darcy's Law applied to trees (Whitehead et al. 1984, Whitehead 1998):

$$k_l = \frac{k_s A_s}{h \eta A_l}, \quad (3)$$

where k_s is specific conductivity of the xylem, A_s is sapwood area, A_l is leaf area and η is the viscosity of water. If all components are constant except for h, then Equation 3 reduces to $k_l = 1/h$, which takes the shape of a nonlinear decline, similar to that found by Mencuccini and Grace (1996*a*).

The specific tests of the hydraulic limitation hypothesis that we applied are derived from Ryan and Yoder (1997) and Hubbard et al. (1999), and are modified to include three height classes, using Equations 3 and 4. The hypothesis tests are as follows: (1) k_l is inversely proportional to h; (2) g_s and A decline with increasing h; and (3) the decline in tree growth efficiency (see definition below) is proportional to the decline in A.

Hydraulic compensation

The theoretical basis for hydraulic compensation is presented in Equation 3. A similar derivation of Darcy's Law for g_s can be written in which the soil-to-leaf water potential difference ($\Delta\Psi$) is explicit (Whitehead and Hinckley 1991):

$$g_s = \frac{k_s A_s \Delta\Psi}{h \eta A_l D}. \quad (4)$$

In this case, the denominator from Equation 1 is expressed as $\Delta\Psi/h$, the soil-to-leaf water potential gradient (with the gravitational component removed as in Equation 1), and all other variables are defined as above. This derivation shows that, like k_l, g_s is inversely related to height if all other variables remain constant.

However, if all other variables do not remain constant, then compensation for h may occur. Decreasing the leaf area to sapwood area ratio (A_l/A_s) or increasing k_s may balance the effect of h on k_l; additionally, increasing $\Delta\Psi$ may balance the effect of h on g_s. If compensation is complete, via changes in these variables, then there will be no decline in g_s or k_l with increasing h. Our specific tests for hydraulic compensation are: (1) for compensation to exist, we must observe a decrease in A_l/A_s, or an increase in k_s or $\Delta\Psi$ with increasing h; and (2) for compensation to be complete, we must observe no decline in k_l with increasing h. To examine further the importance of compensation for hydraulic limitations, we compared measured k_l and g_s values with those predicted by Equations 3 and 4 with and without changes in compensating variables.

Table 1. Symbols, definitions and units of terms used in this paper.

Symbol	Description	Units
$\delta^{13}C$	Stable carbon isotope ratio of foliage cellulose	‰
$\delta^{13}C_a$	Stable carbon isotope ratio of atmospheric CO_2	‰
Δ	Carbon isotope discrimination	‰
Ψ_{leaf}	Leaf water potential	MPa
Ψ_{soil}	Soil water potential	MPa
$\Delta\Psi$	$\Psi_{soil} - \Psi_{leaf}$	MPa
η	Dynamic viscosity	kg m^{-1} s^{-1}
A	Net carbon assimilation rate (photosynthesis)	μmol m^{-2} s^{-1}
A_t	Lumen area	μm^2
A_l/A_s	leaf area/sapwood area ratio (shoots or trees)	m^2 cm^{-2}
C_i	Foliar internal CO_2 concentration	Pa
D	Vapor pressure deficit	kPa
D_a	Mean (arithmetic) tracheid diameter	μm
D_{95}	Mean tracheid diameter in which 95% flow occurs	μm
D_h	Hydraulic mean diameter of tracheids	μm
g_s	Stomatal conductance	mol m^{-2} s^{-1}
k_{sp}	Potential saturated hydraulic conductivity	kg m^{-1} s^{-1} MPa^{-1}
k_l	Hydraulic conductance	mmol m^{-2} s^{-1} MPa^{-1}
LAI	Leaf area index	m^2 m^{-2}
[N]	Nitrogen concentration	g g^{-1}
SLA	Specific leaf area	cm^2 g^{-1}

A few additional points must be made regarding the use of Equations 1–4 for development of the hydraulic limitation and hydraulic compensation hypotheses. If the midday maximum $\Delta\Psi$ changes, this will violate an assumption of the hydraulic limitation hypothesis by disrupting the linear relationship between k_l and g_s. Furthermore, increasing $\Delta\Psi$ by lowering Ψ_{leaf} (if Ψ_{soil} is relatively constant) may cause xylem embolism and effectively reduce k_s. Embolism probably occurs routinely in these trees and may vary with tree height (Domec and Gartner 2001), making the assumption that resistance increases linearly with h potentially invalid. Lastly, hydraulic resistance and compensation may also occur in branches (Waring and Silvester 1994), below ground (Sperry et al. 1998, Magnani et al. 2000), or elsewhere. However, we use h as a surrogate for the many resistances from root to leaf for these equations and for the remainder of this paper because h is a significant fraction of total path length and because measurements of total path length were not available. Similarly, compensating mechanisms may exist besides those presented here; therefore, failure to observe changes in the variables listed under test (1) of the hydraulic compensation hypotheses would not necessarily mean that compensation at the whole-tree level does not exist.

Methods

Site description

The study was performed in three stands of Douglas-fir located within the Wind River basin of the Cascade Mountains near Carson, Washington (45°49′ N, 121°57′ W). This region has a maritime climate, with cool wet winters and warm dry summers. Annual precipitation is approximately 2500 mm, of which less than 10% falls between June and September (~120 mm). The soils are loamy sands and sandy loams over 2 to 3 m of volcanic tephra. The stands were within 10 km and 200 m elevation of each other and are described in greater detail in Phillips et al. (2002). The mean height and age of the stands were 15 m and 20 years, 32 m and 40 years, and 60 m and > 450 years. The 20- and 40-year-old stands originated after clear-cuts, whereas the > 450-year-old stand originated after a stand-replacing fire (Franklin and DeBell 1988). Canopy access towers were erected in the center of the 15- and 32-m stands, and a construction crane was used for crown access in the 60-m stand. Four to five trees, and their subtending branches that were typical of each stand were selected. Foliage was measured on three branches per tree in each stand. Sap flow was measured in the same trees (Phillips et al. 2002). Further stand and tree data are provided in Table 2.

Growth efficiency

Growth efficiency, defined as stemwood carbon production per unit leaf area per year (Waring et al. 1980), was measured to determine if the Douglas-fir trees were growing more slowly as they aged, and to determine whether growth declined concurrently with reductions in A. Growth efficiency is a useful measure because it standardizes stemwood growth to the amount of leaf area held by each tree, allowing comparisons among trees of different sizes with different amounts of leaf area (Waring et al. 1980, Yoder et al. 1994, Ryan et al. 1997). Although stemwood growth per unit ground area has often been shown to decline with stand age, this is an inappropriate measure for individual tree-level tests, particularly in old forests of the Pacific Northwest in which Douglas-fir is replaced by other late-successional species (Franklin and

Table 2. Site and tree characteristics. Abbreviation: na = data not available.

Height (m)	Age (year)	Density > 5 cm (trees ha^{-1})	LAI_s[d]	LAI_i[e]	SLA[f] ($cm^2\ g^{-1}$)	Foliar [N][g] ($g\ g^{-1}$) (SE)	Ring width (mm)	Leader height (m)
15	20	21250[a]	6.1	10.6	60/44	1.03 (0.02)	4.4	0.96
32	40	1420[b]	5.6	na	71/47	1.48 (0.03)	2.3	0.93
60	450	448[c]	8.6	na	69/39	0.76 (0.08)	0.8	0.06[h]

[a] Data from 12, 10 × 10 m plots, all trees > 2.5 cm DBH.
[b] Data from Chen et al. (2000).
[c] Data from Wind River Canopy Crane Research Facility.
[d] Stand-level leaf area index. Note that LAI of Douglas-fir in the 32-m stand is approximately 5, and in the 60-m stand is only 2.5. The remaining leaf area is dominated by western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata* J. Donn ex D. Don) and understory plants.
[e] Patch-level leaf area index in the immediate vicinity of the sample trees, approximately 100 m^2 ground area.
[f] Mean specific leaf area of foliage from the entire canopy and mean specific leaf area of foliage from gas exchange, nitrogen and carbon isotope measurements (i.e., entire canopy/canopy top). The canopy mean SLA is from branch harvests throughout the vertical profile of the canopy and includes all age classes (N.G. McDowell et al., unpublished data). Canopy-top SLA is for foliage that elongated in 1998.
[g] Foliar [N] from 1-year-old foliage that elongated in 1998.
[h] For the 60-m site, mean heights of 1998 leaders of Douglas-fir are from Ishii et al. (2000).

DeBell 1988; for example, Douglas-fir comprises < 30% of the basal area in the 450-year-old forest included in our study). Growth efficiency was determined on five or six trees per stand. Increment cores were taken from the four cardinal directions of each tree for ring width measurement (Table 2). Mean ring widths of individual trees for 1994–1999 were used to calculate stemwood production from an allometric equation for Douglas-fir (Gholz et al. 1979), assuming that stemwood dry matter was 50% carbon. Whole-tree leaf area was determined for each of the cored trees with site- and age-specific allometric equations that predict whole-tree leaf area from sapwood area at 1.3 m (McDowell et al. 2002). The individual tree was the sample unit for growth efficiency.

Gas exchange

Diurnal gas exchange (water vapor and carbon dioxide) was measured at each stand in July, August and September 1999. Gas exchange was measured with an LI-6400 portable photosynthesis system (Li-Cor, Lincoln, NE) equipped with a blue–red artificial light source. Cuvette irradiance was 1400 μmol $m^{-2}\ s^{-1}$; photosynthesis in the upper crown of Douglas-fir saturates at 1000 μmol $m^{-2}\ s^{-1}$ (Lewis et al. 1999). Cuvette CO_2 was 40 Pa. Cuvette and leaf temperature were allowed to track ambient temperature, with values ranging from 22 to 34 °C depending on the time of year. Leaf temperature within the cuvette was typically within 1 °C of ambient temperature outside the cuvette, with extreme deviations up to 2.5 °C. Cuvette humidity was typically within 5% of ambient humidity, which varied from 16 to 61%. Hourly measurements were made on 1-year-old foliage within the top 10% of the live crown and from all aspects of the trees from ~0700 h until mid- or late-afternoon unless excessive winds made use of the canopy crane impossible. One shoot per branch per day was measured repeatedly, and we typically made measurements on three branches per tree. Because of the distance between sites and the logistics of working in tall towers or the crane, it was not possible to measure all sites in a single day. Therefore, trees at different sites were measured on successive days with similar weather to minimize confounding of site comparisons with time. Foliage was not measured unless it had been in full sunlight for at least 20 min prior to measurement. Vapor pressure deficit near the same canopy height at which the gas exchange measurements were made was calculated from air temperature and humidity (Phillips et al. 2002) measured concurrently with gas exchange.

To determine if A and g_s declined with increasing size, we compared the slopes of A and g_s versus D for each site by analysis of covariance. Comparing the slopes rather than the mean daily values of g_s and A is necessary because of the strong effect of D on g_s, transpiration and A (Monteith 1995, Hubbard et al. 1999). Stomatal conductance should be related nonlinearly and negatively to tree D, as predicted by Equation 4. However, we observed a linear, rather than nonlinear, relationship, and thus used linear analysis of covariance. We used individual shoots as our sampling unit for A and g_s.

Water potential

We measured Ψ_{leaf} concurrently with each gas exchange measurement with a Scholander-type pressure chamber (PMS, Corvallis, OR) on small shoots neighboring the shoot used for gas exchange measurements. We estimated Ψ_{soil} in the root zone from measurements of predawn unbagged Ψ_{leaf} of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) saplings located in the 15- and 32-m stands and of western hemlock trees in the 60-m stand. We duplicated the test of Bauerle et al. (1999) and found that the predawn water potential of hemlocks was identical to that of overstory Douglas-fir trees after correction for the gravitational gradient (0.01 MPa m^{-1}, $P = 0.27$, $n = 3$). We assumed that nighttime transpiration was negligible. Shoots from individual trees were our sampling unit for Ψ_{leaf}.

Hydraulic conductance

Leaf-specific hydraulic conductance was calculated from Equation 1. Measured values from which k_l was calculated included g_s, Ψ_{leaf} and Ψ_{soil}, and estimates of foliage height above

ground. Measurements were made over one daylight period at each of the three stands in July, August and September 1999. In some cases, k_l was positively related to D at low values of D (< 1.0 kPa, results not shown). Therefore, we present mean values of k_l from periods of equal sample size (36 leaf-level measurements per site) and similar D (0.5 to 1.0 kPa, 1.25 to 1.75 kPa, and 2.25 to 2.75 kPa). We used individual shoots as our sampling unit for k_l. Similar estimates of k_l at the whole-tree scale, from sap flow measurements, are described in a related study by Phillips et al. (2002).

Carbon isotopes

We utilized carbon isotope discrimination (Δ) from canopy-top foliage as an independent test of the hypothesis that g_s declines with increasing height. Discrimination, which we calculated from the stable carbon isotope ratio ($\delta^{13}C$) of foliar cellulose, is an assimilation-weighted index of g_s if photosynthetic capacity, light availability and source air $\delta^{13}C$ are similar or known. A subset of foliage on which gas exchange was measured was used for $\delta^{13}C$ analysis. Cellulose was extracted by the method described by Wise et al. (1946). Cellulose $\delta^{13}C$ was analyzed with an isotope ratio mass spectrometer at the Idaho Stable Isotope Laboratory (Moscow, ID). Standard deviations around the in-lab $\delta^{13}C$ flour standards averaged 0.10‰ (n = 17), and those around a separate $\delta^{13}C$ pine standard were 0.09‰ (n = 6). Because this foliage was extracted from well-ventilated sun-exposed branches near the top of each tree, we assumed that light availability was similar across sites. Independent measurements of atmospheric $\delta^{13}CO_2$ ($\delta^{13}C_a$) at the canopy top showed no difference among stands (Fessenden and Ehleringer 2002). Therefore, we calculated Δ from site-specific values for cellulose $\delta^{13}C$ and a $\delta^{13}C_a$ value of −8.00‰ (Farquhar et al. 1989):

$$\Delta = (\delta^{13}C_a - \delta^{13}C)/(1 + \delta^{13}C/1000). \quad (5)$$

The relationship between Δ and tree height should be negative and nonlinear if photosynthetic capacity is constant and g_s declines with height as predicted by the hydraulic limitation hypothesis and Equation 4. We used foliage from individual trees as our sampling unit for Δ.

Photosynthetic capacity

We estimated foliar photosynthetic capacity in two ways. Foliar nitrogen concentration [N] was measured because it is strongly related to photosynthetic capacity (Field and Mooney 1986, Livingston et al. 1998). Second, photosynthetic capacity was assessed by means of response curves of photosynthesis to internal [CO_2] (A/C_i curves). Foliar [N] was obtained from a subset of whole-foliage samples collected after gas exchange measurements. Samples were dried at 65 °C for 48 h, ground with a mortar and pestle and analyzed with a LECO CNS 2000 (LECO, St. Joseph, MI). The A/C_i curves were constructed from measurements on five 32-m trees and four 60-m trees made on overcast days between June 22 and 29, 1999, and on five 15-m trees on July 21, 1999. Cuvette conditions were the same as those described above for gas exchange measurements. The A/C_i curves were generated by changing the cuvette CO_2 in the following order: 40, 30, 20, 10, 40, 60, 80, 100, 120, 160 and 200 Pa. After each exposure to a new CO_2 partial pressure, foliar A was allowed to reach steady state (cuvette CO_2 coefficient of variation < 2%) prior to measurement. Six measurements were made per sample per CO_2 partial pressure over a 60-s period after steady state had been reached. The maximum carboxylation rate and maximum electron transport rate were calculated from the A/C_i curves by means of nonlinear least squares regression to fit the values of these parameters to the best fit equations of the photosynthesis model of von Caemmerer and Farquhar (1981) (Harley et al. 1992).

Sapwood-specific hydraulic conductivity

We measured sapwood anatomy for estimation of potential saturated hydraulic conductivity (k_{sp}; kg m^{-1} s^{-1} MPa^{-1}) on shoots from the 15- and 60-m trees, and from boles of the 15-, 32- and 60-m trees. Five shoots were harvested, one per tree, from upper canopy branches at sunrise (typically before 0700 h) and again at 1500 to 1700 h. Shoots were typically 0.5 to 2.0 cm in diameter. We placed the samples under a gravitational pressure potential of 0.01 MPa with filtered (0.22 μm) 0.5% safranin dye and allowed the dye to perfuse for 30 min. Three cross-sectional samples were sectioned with a sliding microtome and fixed on glass slides with 70% ethyl alcohol. Stained sapwood and tracheid lumen areas were determined with a digital imaging and analysis system (Sony CCD/RGB Color Video Camera, Nikon Labophot-2 compound microscope and NIH Image (public domain image processing and analysis program), Version 1.59). Lumen areas were measured on three subsamples per cross section distributed across the outside pith radius of the shoot. For the 60-m trees, the three subsamples were typically located on the second, fifth and ninth rings from the pith, and for the 15-m trees, the subsamples were located on the first, second and occasionally the third rings from the pith. Stained sapwood and vessel density were determined as a proportion of total sapwood area. We estimated native cavitation as the percent difference between stained sapwood area and total sapwood area, not including the pith area (Panek and Waring 1995). Shoots from the 60-m stand were, on average, 10 years old, whereas the shoots from the 15-m stand were typically 3 years old.

Anatomy of bole sapwood was examined by means of a technique similar to that described above for shoots. Sapwood cores were collected at a height of approximately 1.4 m on five trees per site with increment borers. One core was collected per tree. Lumen areas were typically measured on two or three of the outermost rings on each core, and were distributed approximately evenly between earlywood and latewood.

Vessel density and lumen areas within the sapwood were used to estimate k_{sp} according to Poiseuille's law:

$$k_{sp} = (\pi/8\eta(\sum r^4))/A_s, \quad (6)$$

where r is the radius of a circle having the same area as the cor-

responding tracheid and A_s is sapwood area. This is considered an estimate of maximum potential conductivity because it assumes no differences in tracheid length or friction due to bordered pits, tracheid tapering or xylem cavitation.

Leaf area/sapwood area

Shoot-level A_l/A_s was measured on shoots collected in July 2000. Shoots that were at least 0.5 cm in diameter were collected from five trees per stand at the 15- and 60-m stands. Shoots were obtained from the upper 10% of the crown of each tree, from all aspects. Leaf area was measured on all foliage from the shoots. Whole-tree A_l/A_s was obtained from five or six trees per site as described by McDowell et al. (2002), the results of which are provided in Table 3.

Statistical analysis

All data used to test the hydraulic limitation and hydraulic compensation hypotheses were collected between June and September 1999, with the following exceptions: Ψ_{soil} and Ψ_{leaf} data were collected in both 1998 and 1999, and shoot-level vascular anatomy, A_l/A_s and cavitation were measured between June and September 2000. Statistical analyses were performed with Systat 9.0, with an alpha level of 0.05. Post-hoc analyses were performed after detection of significant differences by means of a Tukey's highest significant difference test for pair-wise differences (Neter et al. 1990). Analysis of covariance was used to compare the slopes of A and g_s versus D. Repeated measures analysis of covariance was used for data collected from the same trees repeatedly over time. Data met the assumptions of normality and homogeneity of variance as examined with scatterplots and histograms of the residuals.

Results

Stemwood growth efficiency declined in a nonlinear fashion with increasing tree height (r^2 = 0.68, Figure 1). Stemwood growth efficiency averaged 59.8, 34.7 and 27.9 g C m^{-2} leaf area per year for the 15-, 32- and 60-m trees, respectively. Height growth averaged nearly 1 m $year^{-1}$ for the 15- and 32-m trees, and only 0.06 m $year^{-1}$ for the 60-m trees (Table 2).

There was no statistically significant difference in the slope of A versus D between stands (P = 0.08, Figure 2a). Similarly, there was no statistical difference in the slope of g_s versus D between stands (P = 0.32, Figure 2b).

The $\delta^{13}C$ values of cellulose extracted from canopy-top foliage increased (i.e., became less negative) with increasing tree size. The $\delta^{13}C$ values differed significantly with height class (polynomial contrast $P < 0.001$). Carbon isotope discrimination calculated from Equation 5 averaged 18.6, 17.6 and 15.9‰ for the 15-, 32- and 60-m trees, respectively (polynomial contrast $P < 0.001$, Figure 3). Foliar [N] at canopy tops was different between each size class ($P < 0.001$) but was not correlated with height. Foliar [N] was highest at the 32-m stand (1.48%), intermediate at the 15-m stand (1.03%), and lowest at the 60-m stand (0.76%, Table 2). The maximum carboxylation rates, calculated from the A/C_i curves, were 27.5, 47.9 and 38.9 μmol m^{-2} s^{-1} for the 15-, 32- and 60-m trees, respectively (P = 0.01). The maximum electron transport rates were 97.9, 147.4 and 128.7 μmol m^{-2} s^{-1} for the 15-, 32- and 60-m trees, respectively (P = 0.03). There was no relationship between Δ and photosynthetic capacity as indexed with foliar [N] (P = 0.56). Likewise, there was no relationship between Δ and carboxylation rates or electron transport rates (P = 0.82 and 0.90, respectively).

Leaf specific hydraulic conductance, calculated from Equation 1, was not statistically related to D for any of the height classes ($P > 0.1$). Mean k_l of the 32- and 60-m trees were 0.87 and 0.82 mmol m^{-2} s^{-1} MPa^{-1}, respectively, and were statistically identical (P = 0.79). Hydraulic conductance of the 15-m trees averaged 1.56 mmol m^{-2} s^{-1} MPa^{-1} and was significantly higher than k_l of the taller trees ($P < 0.01$, Figure 4).

Predawn Ψ_{soil} was not significantly different across tree size classes (repeated measured ANOVA, P = 0.54 and 0.87 for 1998 and for 1998–1999 combined, respectively) except for September 1999, at which time Ψ_{soil} in the 15-m stand was significantly more negative than in the other two stands ($P <$ 0.01). Trees in all stands showed a characteristic threshold minimum midday Ψ_{leaf}, and for the 15- and 32-m trees this

Table 3. Anatomical and structural characteristics of tree height classes. Within the subheadings Shoot and Bole, values followed by the same letter are not significantly different between height classes at $\alpha = 0.05$. Potential saturated hydraulic conductivity (k_{sp}) was calculated from Equation 6; A_t = measured lumen area; D = diameter calculated from measured A_t values; tracheid number is per unit sapwood area; and A_l/A_s is leaf area/sapwood area ratio.

Height (m)	Sample	k_{sp} (kg m^{-1} s^{-1} MPa^{-1})	A_t (μm^2)	D_a[1] (μm)	D_h[2] (μm)	Tracheid no. (no. mm^{-2})	A_l/A_s[3] (m^2 cm^{-2})
15	Shoot	1.17 a	75.1 a	9.4 a	11.29 a	4280 a	1.21 a
60	Shoot	0.84 a	53.3 b	7.9 b	10.46 b	6048 b	0.97 b
15	Bole	11.70 a	520.2 a	25.3 a	29.6 a	1025.1 a	0.51 a
32	Bole	16.95 a	565.1 a	24.6 a	31.9 a	947.5 a	0.49 a
60	Bole	14.51 a	716.3 a	27.0 a	36.6 a	650.4 b	0.39 b

[1] Mean diameter of tracheids calculated as the arithmetic mean.
[2] Hydraulic mean diameter, equivalent to $\Sigma diameter^4/\Sigma diameter^5$ (Pockman and Sperry 2000).
[3] Whole-tree A_l/A_s from McDowell et al. (2002).

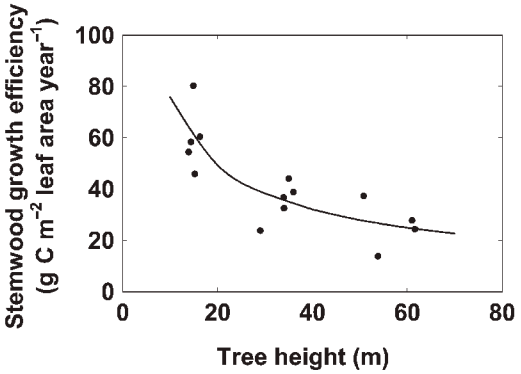

Figure 1. Stemwood growth efficiency, defined as stemwood growth per whole-tree leaf area, versus tree size. Individual trees are plotted. The equation of the line is: growth efficiency = 317.34(height)$^{-0.62}$, $r^2 = 0.68$.

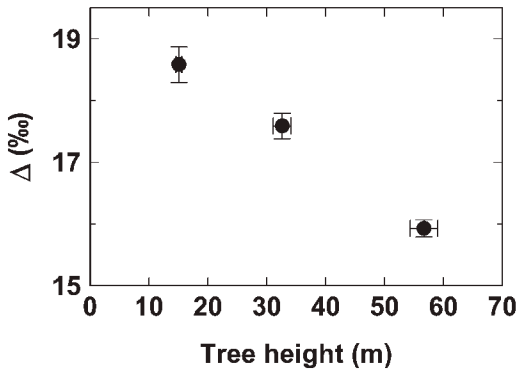

Figure 3. Carbon isotope discrimination (Δ) of upper canopy foliage versus tree height for Douglas-fir trees. Values are the mean of 10 or more foliage samples per stand. Bars are standard errors.

minimum was approximately –2.1 MPa. However, the 60-m trees had more negative midday Ψ_{leaf} than the 15- or 32-m trees in both 1998 and 1999 (repeated measures ANOVA, $P < 0.001$ for both, Figures 5a and 5b), reaching daily mean values of –2.6 MPa. The soil-to-leaf water potential difference, estimated as mean $\Psi_{soil} - \Psi_{leaf}$ for the corresponding days, was consistently larger for the 60-m trees (repeated measures ANOVA, $P < 0.01$, Figures 5c and 5d). Values of $\Delta\Psi$ did not differ between the 15- and 32-m trees when compared over the entire season ($P = 0.29$).

Shoot-level A_l/A_s decreased with increasing tree size, averaging 1.21 and 0.97 m^2 cm^{-2} for the 15- and 60-m trees, respectively (*t*-test: $P = 0.02$; Table 3). This 20% decline in shoot-level A_l/A_s was similar in magnitude to the decline in A_l/A_s of whole trees. Whole-tree A_l/A_s declined by 25% between the 15- and 60-m trees (from 0.51 to 0.39 m^2 cm^{-2}; McDowell et al. 2002). Mean lumen area of shoot xylem from the 60-m trees was significantly lower than for the 15-m trees (53.3 and 75.1 μm^2, respectively; $P = 0.02$, Table 3). Lumen diameters were smaller for shoots of 60-m trees than shoots of 15-m trees, independent of the method of calculation ($P < 0.02$, Table 3). The mean number of tracheids per unit sapwood area was also significantly higher for shoots of 60-m trees compared to those of 15-m trees ($P = 0.001$, Table 3). Despite the substantial differences in vascular anatomy between

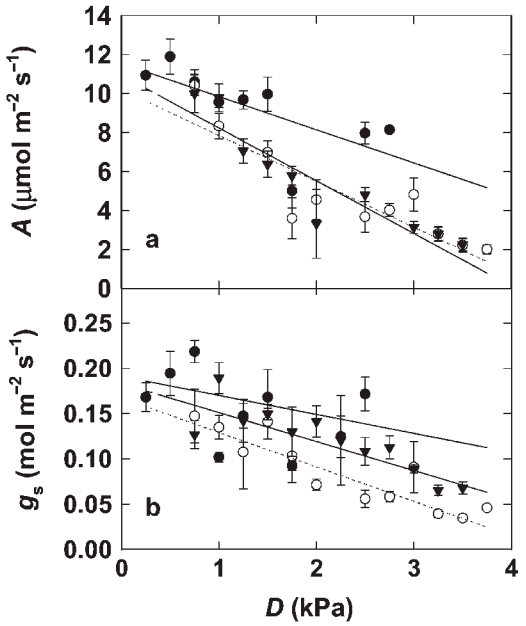

Figure 2. (a) Stomatal conductance (g_s) and (b) net photosynthesis (A) versus vapor pressure deficit (D) of Douglas-fir trees with heights averaging 15 m (—, ●), 32 m (·····, ○) and 60 m (– – –, ▼). Data were collected between July and September 1999. Values were binned by 0.25 kPa classes of D for presentation. Regression lines were not significantly different from each other, and are shown only to aid in identifying data from each height class. Foliage was the sample unit. Bars are standard errors.

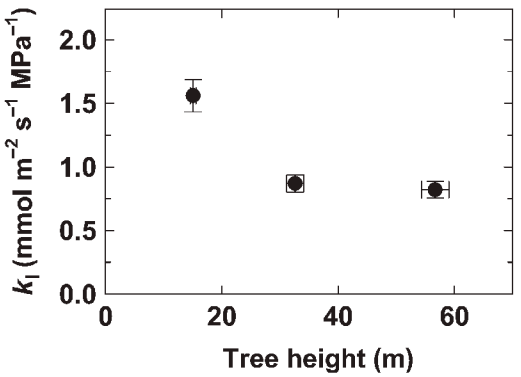

Figure 4. Leaf-specific hydraulic conductance (k_l) versus tree height for Douglas-fir trees. Values are mean measured k_l averaged between July, August and September 1999. Foliage was the sample unit and bars are standard errors.

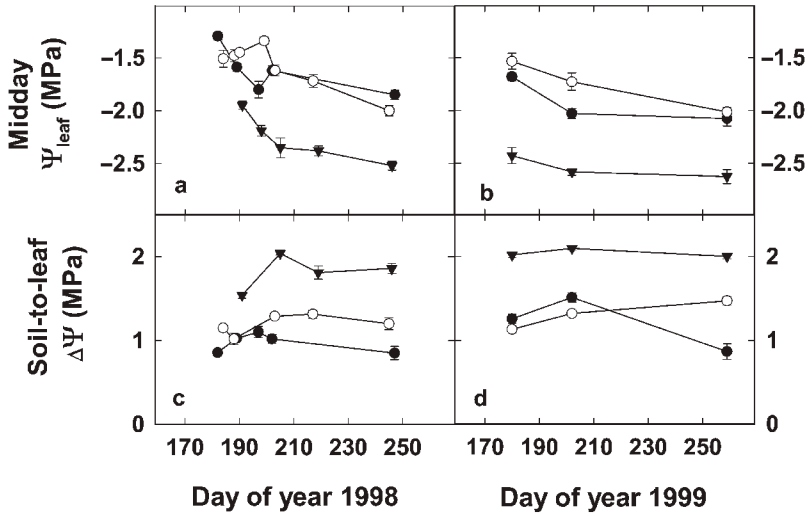

Figure 5. Water potential of 15-, 32- and 60-m tall Douglas-fir trees. (a, b) Midday water potential (Ψ_{leaf}) for 1998 and 1999. (c, d) The soil-to-leaf water potential difference ($\Delta\Psi$), calculated as $\Psi_{soil} - \Psi_{leaf}$, for 1998 and 1999. Soil water potential data are provided in Phillips et al. 2002. The shoot is the sample unit. Bars are standard errors of shoot-level measurements for Ψ_{leaf}. The Ψ_{leaf} measurements were averaged between 1200 and 1500 h on each date.

tree size classes, calculated shoot k_{sp} (Equation 6) was not significantly different between 15-m trees (1.17 kg m^{-1} s^{-1} MPa^{-1}) and 60-m trees (0.84 kg m^{-1} s^{-1} MPa^{-1}; $P = 0.11$, Table 3). At the bole level, the number of tracheids per unit sapwood area was the only anatomical measurement that differed significantly between height classes, with the 60-m trees having significantly lower values than the 15- and 32-m trees ($P = 0.01$, Table 3). The number of tracheids per unit sapwood area did not differ between 15- and 32-m trees ($P = 0.77$, Table 3). The lower number of tracheids per unit sapwood area in the bole sapwood of the 60-m trees counteracted the slightly larger lumen areas (Table 3), resulting in similar estimates of k_{sp} of bole sapwood between size classes ($P = 0.33$, Table 3).

The proportion of sapwood conductive to water was consistently less for shoots of the 60-m trees than for shoots of the 15-m trees throughout the summer of 2000 ($P < 0.001$, Figure 6). The proportion of functional sapwood did not differ between shoots collected at dawn and those collected in the late afternoon ($P = 0.37$). Likewise, there were no differences in the proportion of functional sapwood of shoots across months ($P = 0.19$).

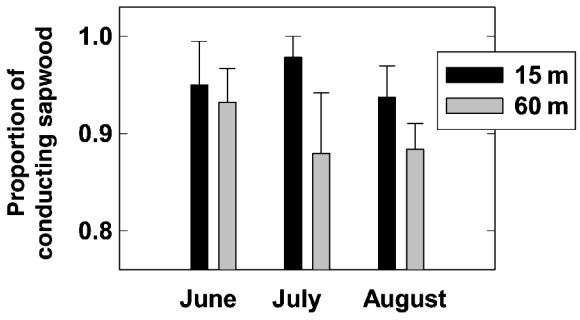

Figure 6. Proportion of conducting sapwood of shoots from 15- and 60-m tall Douglas-fir trees. Functional sapwood was measured by dye perfusion. The individual shoot is the sampling unit. Bars are standard errors.

We modeled k_l from Equation 3 with measured values of whole-tree A_l/A_s and $\Delta\Psi$ for all tree height classes (Figure 7a, solid line). The model predictions were within 9% of the measured values when A_l/A_s and $\Delta\Psi$ were allowed to vary with tree size ($R^2 = 0.99$, $P = 0.03$). To examine the effect of compensating mechanisms on k_l, we remodeled k_l, holding either A_l/A_s constant at the mean value of the 15-m trees (maximum A_l/A_s, dotted line), $\Delta\Psi$ constant at the mean value of the 15-m trees (minimum $\Delta\Psi$, dashed line), or both A_l/A_s and $\Delta\Psi$ constant at the mean value of the 15-m trees (maximum A_l/A_s, minimum $\Delta\Psi$, dashed and dotted line). We chose not to model the effect of changing k_{sp} because no statistical differences were found between k_{sp} of 15- and 60-m trees. Values of k_l for each tree, obtained from Equation 3, were divided by the value of the shortest tree and then multiplied by k_l of that tree (as in Schäfer et al. 2000). This standardized k_l of all trees, assuming that k_l of the larger trees was similar to that of the smaller trees when they themselves were smaller. Assuming that A_l/A_s does not vary with height cause the model to underestimate k_l by 6 and 18% for the 32- and 60-m trees, respectively. Assuming that $\Delta\Psi$ does not change with height caused the model to underestimate k_l by 22 and 38% for the 32- and 60-m trees, respectively. Finally, assuming that neither A_l/A_s nor $\Delta\Psi$ change with height caused the model to underestimate k_l by 27 and 54% for the 32- and 60-m trees, respectively.

Equation 4 was used to predict g_s (Figure 7b) because measured and modeled values of k_l are not fully independent (they share $\Delta\Psi$), whereas measured and modeled values of g_s are fully independent. This model was run identically to that presented in Figure 7a, except that mean cuvette-based g_s measured in July was used as the dependent variable. July g_s measurements were used because similar environmental conditions existed across the three sites only for samples from this month. When A_l/A_s and $\Delta\Psi$ were allowed to vary with tree

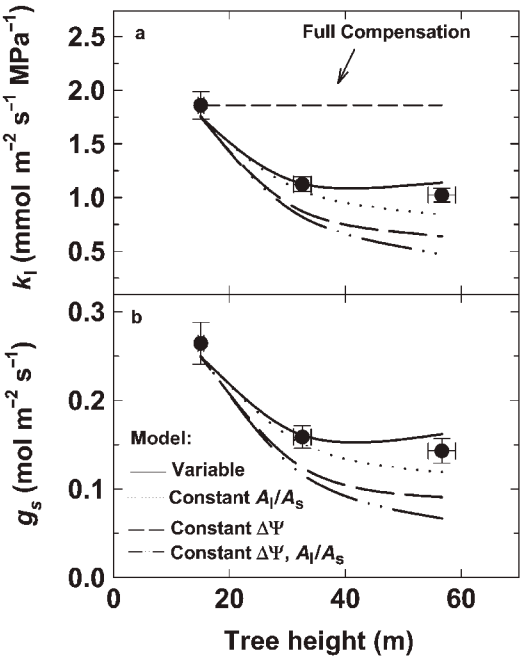

Figure 7. (a) Mean leaf-specific hydraulic conductance (k_l) averaged over the year versus tree height. (b) Mean stomatal conductance (g_s) measured in July versus tree height. July g_s data were used because this was the only sample period when D was similar across height classes. Standard error bars are provided for measured data in both panels. The solid trace (variable) is the hydraulic model (Equation 3 or 4) using measured values of A_l/A_s and $\Delta\Psi$ for all trees. The dot trace is the same model, except A_l/A_s is held constant at the mean value of the 15-m-tall trees. The dash trace is the same model, except $\Delta\Psi$ is held constant at the mean value of the 15-m-tall trees. The dash/dot trace is the same model assuming no compensation by A_l/A_s or $\Delta\Psi$. The dashed line at the top of the figure is the hypothesized relationship between k_l and tree height if compensation fully balances hydraulic constraints.

size, model predictions were within 5% of measured g_s for the 15- and 32-m trees, and within 13% of measured g_s for the 60-m trees ($R^2 = 0.97$, $P = 0.08$). Assuming that A_l/A_s does not vary with height caused the model to underestimate g_s by 17% for the 60-m trees. Assuming that $\Delta\Psi$ does not change with height caused the model to underestimate g_s by 36% for the 60-m trees. Finally, assuming that neither A_l/A_s nor $\Delta\Psi$ change with height caused the model to underestimate g_s by 53% for the 60-m trees.

Discussion

Evidence for and against the hydraulic limitation hypothesis

Contrary to predictions of size-related hydraulic limitation to gas exchange, we found that (1) cuvette-based g_s and A did not differ with height when compared across a range of D (Figures 2a and 2b), and (2) the lack of difference in cuvette-based A (Figure 2a) means that the decline in growth efficiency (Figure 1) cannot be explained by a decline in A. On the other hand, the k_l and Δ results conformed to predictions of the hydraulic limitation hypothesis. We suspect that the cause of these mixed results is one of the following scenarios: (1) the important period for manifestation of hydraulic constraints to carbon gain occurs in the pre-drought months (before July) and thus the appropriate time to test for hydraulic limitation is in the spring months, or (2) hydraulic limitations to gas exchange are not operating in this system, and Δ is controlled by some factor other than g_s.

In reconciling our cuvette-based g_s measurements with g_s inferred from Δ, we have been led to hypothesize that hydraulic limitations to gas exchange may occur in the spring months but not during summer drought. The cellulose carbon from which $\delta^{13}C$ was measured was laid down when foliage elongated in May 1998, whereas the cuvette data were collected from fully elongated, 1-year-old foliage in July, August and September 1999. This temporal discrepancy could cause physiological differences as a result of the different years (1998 versus 1999) and different seasons (spring versus summer). A difference between years is important to consider; the $\delta^{13}C$ data were derived from foliage that elongated in May 1998, a month with substantially above-average precipitation (NOAA, www.ncdc.gov; Oregon Climate Service, www.ocs. orst.edu), whereas the cuvette data were collected during a period of below-average precipitation in mid-summer 1999. In addition, the progressive drought that occurs in the Pacific Northwest causes spring months to have relatively high soil and atmospheric water contents, which decline as the summer drought progresses. If both the Δ and cuvette data are correct, then perhaps stomatal limitations associated with height are manifest during periods of high water availability, but such limitations are overwhelmed by drought conditions. In support of this hypothesis, cuvette-based C_i in July was closer to that predicted by cellulose $\delta^{13}C$ ($r^2 = 0.87$) than by cuvette data from August or September ($r^2 < 0.05$), months with less available soil water (Phillips et al. 2002). Both cuvette and Δ data were derived from the same foliage near the tops of trees, so spatial variation cannot be responsible for the discrepancy between Δ and cuvette-based g_s. As in our study, Bauerle et al. (1999) found no difference in cuvette-based g_s between saplings and old Douglas-fir trees, and a large difference (4.5‰) in $\delta^{13}C$. They concluded that cuvette-based g_s was a poor measure compared with $\delta^{13}C$ data because of the limited temporal integration of gas exchange instruments. Lastly, our limited gas exchange sampling may also have constrained our ability to detect statistical differences in gas exchange across height classes. Despite conducting gas exchange measurements on subsequent days, we obtained relatively little g_s and A data at D values greater than 2 kPa at the 15-m site (Figures 2a and 2b). This poor distribution of data across the range of D may have hampered our statistical ability to discern differences between the 15-m trees and taller trees.

Fessenden and Ehleringer (2002) also measured differences in Δ at both the leaf and ecosystem scales that suggest lower g_s in older stands; however, they too failed to find a strong relationship between stomatal conductance (measured by cuvette

techniques) and Δ. Because soil- and ecosystem-respired $\delta^{13}C$ have been strongly linked to g_s (Ekblad and Högberg 2001, Bowling et al. 2002), the data of Fessenden and Ehleringer (2002) suggest that cuvette-based measurements of g_s may miss height-related patterns in g_s that are manifest at both the leaf and canopy scales.

If the Δ results are an accurate measure of stomatal conductance, then height-related variation in g_s must occur in spring. Eddy covariance measurements have shown that April and May are the months of maximal carbon uptake at the 60-m forest (K.T. Paw U et al., University of California, Davis, unpublished results). Foliar cellulose $\delta^{13}C$ is probably an assimilation-weighted measure of Δ during leaf elongation (Brugnoli et al. 1998, although some amount of carbohydrate stored over winter is possibly incorporated), thus we know that Δ must have varied linearly with height during April and May 1998 (Figure 3). In turn, the Δ results suggest that g_s declines linearly with height because variation in Δ was not a result of photosynthetic capacity or light availability (Farquhar et al. 1989, Livingston et al. 1998). Because spring is the time of maximum carbon assimilation in this forest (K.T. Paw U et al., unpublished data), any height-related reductions in g_s may translate into height-related reductions in gross carbon uptake. Therefore, future tests of the hydraulic limitation hypothesis in coastal Douglas-fir should include intensive sampling in the spring months.

Alternatively, the height-related foliar Δ patterns may be caused by a factor other than stomatal conductance. Although we can only speculate on these mechanisms, they may include differences in (1) the occurrence of freezing between sites, (2) stomatal sensitivity to freezing, (3) photosynthetic capacity during the period before and during leaf elongation, or (4) mesophyll resistance.

Hydraulic conductance declined with tree height in a manner similar to that predicted by Equation 3 (Figure 4). This supports the hypothesis that height is an important factor governing k_l. The decline in k_l parallels the decline in growth efficiency (Figure 1). However, k_l declined less in tall trees than was predicted by Equation 3 (Figure 7a), suggesting that hydraulic compensation occurred.

Evidence for and against the hydraulic compensation hypothesis

Evidence for hydraulic compensation is found in the fit, or lack thereof, of predictions from Equations 3 and 4 to the measured k_l and g_s data in the four scenarios presented in Figures 7a and 7b. The model underestimated k_l and g_s in 60-m trees by 18 to 61%, when A_l/A_s or $\Delta\Psi$ were not allowed to vary with height. A similar result was found in *Fagus sylvatica* L. by Schäfer et al. (2000), where height-related reductions in crown conductance were minimized by concurrent reductions in A_l/A_s. This evidence for the existence of hydraulic compensation supports the ideas of Mencuccini and Grace (1996*b*), Meinzer et al. (1997), Ryan and Yoder (1997) and Becker et al. (2000). However, because k_l declined with increasing tree height, it is also clear that hydraulic compensation is insufficient to fully mitigate size-related constraints on hydraulic and stomatal conductance (Bond and Ryan 2000, Mencuccini and Magnani 2000).

The results presented in Figures 7a and 7b suggest that increasing $\Delta\Psi$ had a greater effect on the maintenance of k_l and g_s than decreasing A_l/A_s . The concept of increasing $\Delta\Psi$ by decreasing Ψ_{leaf} to compensate for tree size has not been suggested previously. This is partly because of evidence for species-specific values of threshold midday Ψ_{leaf} (e.g., Bond and Kavanagh 1999). Minimum midday Ψ_{leaf} does not vary for large and small ponderosa pine (Yoder et al. 1994, Ryan et al. 2000). However, lower minimum Ψ_{leaf} values were observed with increasing tree height in lodgepole pine (Yoder et al. 1994) and *Eucalyptus saligna* Sm. (Barnard 2001). Hacke et al. (2000) found that Ψ_{leaf} in loblolly pine trees (*Pinus taeda* L.) decreased as soil texture became more coarse, and suggested that this maintains the trees' capacity to extract sufficient water for transpiration. Therefore, a height-related decline in minimum Ψ_{leaf} may be a mechanism for maintaining liquid-phase water flux and thereby minimizing reductions in k_l and g_s as trees grow larger.

The more negative midday Ψ_{leaf} found in tall trees (Figures 5a and 5b) is unlikely to have a direct, positive effect on g_s. However, reducing Ψ_{leaf} may act to minimize height related reductions in g_s by increasing the daily range of Ψ_{leaf}, thereby prolonging the daily period before stomatal closure. The minimum Ψ_{leaf} required to hold a vertical water column is 0.01 MPa m^{-1} above ground; therefore, the least negative water potential a leaf can have at the top of a 60-m tree is –0.60 MPa. If the minimum midday Ψ_{leaf} were invariant with tree height (for example, –2.1 MPa), because g_s declines at a threshold Ψ_{leaf} (Tyree and Sperry 1988, Bond and Kavanagh 1999), the maximum range of Ψ_{leaf} over which foliage at the top of 60-m trees may operate is only 1.5 MPa (–0.6 minus –2.1), whereas for a 10-m tree, the Ψ_{leaf} range is 2.0 MPa (–0.10 minus –2.1). The smaller Ψ_{leaf} range for the large trees should result in a relative reduction in daily g_s because the foliage will reach the threshold Ψ_{leaf} earlier in the day (assuming maximum g_s is invariant with height). However, given the observed Ψ_{leaf} values of –2.6 MPa for the 60-m trees and –2.1 MPa for the 15- and 32-m trees, the potential range over which foliage may operate is actually greatest for the tallest trees, with a range of 2.0 MPa (–0.6 minus –2.6 MPa) versus 1.95 MPa for the 15-m trees (–0.15 minus –2.1 MPa) and 1.78 MPa for the 32-m trees (–0.32 minus –2.1 MPa).

The consequences of decreasing Ψ_{leaf} below tensions at which xylem cavitation occurs are well established (Tyree and Sperry 1988). If increased $\Delta\Psi$ in taller trees compensates for increased path length, it may be at the cost of increased cavitation. We observed significantly less functional sapwood, as indexed by dye perfusion, in the shoots of 60-m trees (Figure 6). The loss of functional sapwood in the 15-m trees was similar to that observed in Douglas-fir in cool, wet coastal locations, whereas that of the 60-m trees was similar to Douglas-fir located in hot, dry inland locations (Panek and Waring 1995). This large difference in conducting sapwood may be partially responsible for the relatively low k_l in the 60-m trees. However, we found a decrease in A_l/A_s in shoots,

which may help maintain k_l during times of cavitation (Phillips et al. 2000).

We expected compensatory increases in k_{sp} with increasing tree size (Pothier et al. 1989, Ryan and Yoder 1997, Becker et al. 2000). Increasing tracheid size is one of the components of cellular anatomy that can increase k_{sp} (Mencuccini et al. 1997). However, we observed no significant change in tracheid lumen area in bole sapwood with tree height, and a decrease in tracheid area of shoot sapwood with increasing height (Table 3). Potential maximum hydraulic conductivity (based on lumen diameters and density) was statistically unrelated to height for both shoot and bole sapwood (Table 3). The decreasing tracheid diameter of shoots may increase xylem resistance to cavitation (e.g., Pockman and Sperry 2000). The greater water tensions experienced by the 60-m trees (Figure 5) and the lower percentage of functional sapwood (Figure 6) may provide the driving force for declining tracheid diameter in the shoots of taller trees. Despite reductions in shoot tracheid size, mean k_s of whole trees may have remained constant or even increased with tree size (Phillips et al. 2002). Other factors are important in controlling k_s, including tracheid length and the permeability of pit membranes (Mencuccini et al. 1997), tracheid tapering (West et al. 1999), and changes in k_{sp} throughout the sapwood continuum from root to shoot (Domec and Gartner 2001, Spicer and Gartner 2001).

Conclusion

Evidence of hydraulic constraints to water transport was observed with height-related reductions in k_l and Δ in Douglas-fir in Wind River, Washington. However, g_s and A did not show height-related differences consistent with the hydraulic limitation hypothesis; therefore, firm conclusions about the hypothesis cannot be made from this study. Further measurements during other parts of the growing season, particularly spring, will be necessary before final conclusions can be drawn. Hydraulic compensation was also observed, but was insufficient to prevent k_l from declining with height. We have demonstrated that constraints to hydraulic conductance can occur in conjunction with hydraulic compensation. Indeed, the simultaneous co-occurrence of hydraulic constraints with compensation suggests that compensation itself may be a response to a hydraulic driving force. The notion that hydraulic systems of trees interact homeostatically to balance the benefits and costs of height growth is not new (e.g., Whitehead et al. 1984, Magnani et al. 2000).

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