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Leaf area compounds height-related hydraulic costs of water transport in Oregon White Oak trees

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Summary

1. The ratio of leaf to sapwood area generally decreases with tree size, presumably to moderate hydraulic costs of tree height. This study assessed consequences of tree size and leaf area on water flux in *Quercus garryana* Dougl. ex. Hook (Oregon White Oak), a species in which leaf to sapwood area ratio increases with tree size. We tested hypotheses that *Q. garryana* individuals of greater size and leaf area show reduced leaf-specific hydraulic conductance (K_L), crown water flux per leaf area (E_L), and carbon isotope discrimination (Δ).

2. K_L, E_L and Δ differed between trees of two size classes examined, with 25 m trees showing evidence of lower water flux and carbon isotopic discrimination compared to 10 m trees. Whole-tree water fluxes were smaller in 25 m than in 10 m trees both per unit sapwood and per leaf area, but more so per unit leaf area: 25 m trees had a leaf to sapwood area ratio 1·6 times greater than that of 10 m trees.

3. The findings from this study are unique in that increased leaf to sapwood area ratio of larger trees compounded hydraulic constraints on water transport due to tree height. These results provide further support and generality to the hypothesis of hydraulic limitations to tree-water flux, and show that limitations to water flux are not necessarily accompanied by the structural compensation of reduced crown leaf area in larger trees.

Key-words: *Quercus*, sap flow, transpiration, xylem

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Introduction

Trees show a variety of structural and anatomical changes that affect their hydraulic function as they grow and age. Decreases in whole-tree hydraulic conductance with increases in tree height and associated hydraulic path length from roots to leaves have been hypothesized to limit tree gas exchange and height growth (Ryan & Yoder 1997). However, size-related changes in tree anatomy and structure could alleviate potential hydraulic restrictions to crown gas exchange in tall trees. For example, taller or older trees may show increased hydraulic conductivity of sapwood (Pothier *et al.* 1989); increased root mass and turnover (Magnani, Mencuccini & Grace 2000); increased access to deep soil water (Dawson 1996); and/or a reduced leaf area to sapwood area ratio ($A_L : A_S$) (McDowell *et al.* 2002a). These factors could, in principle, allow tall trees to maintain stomatal conductance similar to that of smaller trees (Whitehead, Edwards & Jarvis 1984; Becker, Meinzer & Wullschleger 2000; Phillips *et al.* 2000).

Changes in $A_L : A_S$ have a direct effect on potential hydraulic limitations to crown gas exchange. Height-related hydraulic limitations to tree gas exchange may be expected to occur due to reduced leaf specific hydraulic conductance (K_L; mol m^{-2} s^{-1} MPa^{-1}) in taller trees, as seen in the following expression for K_L:

$$K_L = \frac{K}{A_L} = \frac{1}{\sum_i \frac{h_i}{k_{S,i} A_{S,i}}} \cdot \frac{1}{A_L} \qquad \text{eqn 1}$$

where K is whole-tree conductance (mol s^{-1} MPa^{-1}); $k_{S,i}$ is sapwood conductivity (mol m^{-1} s^{-1} MPa^{-1}); h_i is hydraulic path length (m); $A_{S,i}$ and A_L are sapwood and leaf areas, respectively (m^2); and the summation over i is a summation of inverse hydraulic conductivity of

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roots, bole, branches, and the liquid pathway through leaves. In practice, K_L at the organism scale is usually computed as whole-plant transpiration divided by soil to leaf water potential difference (see Methods), and masks the complexity of within-plant variation in k_S and A_S. Nevertheless, equation 1 illustrates that for any portion of the total tree hydraulic pathway, K_L is reduced with path length unless compensating changes in k_S or $A_L : A_S$ occur.

Most, but not all, tree species show the trend of decreasing $A_L : A_S$ with tree size (McDowell *et al.* 2002a). Preliminary measurements in *Quercus garryana* Dougl. ex Hook. (Oregon White Oak) showed that this species has substantially greater $A_L : A_S$ in 25 m tall trees than in 10 m tall trees (Table 1). Little is known about the adaptive significance of increased $A_L : A_S$ with tree size, or its consequences for whole-tree water transport and crown physiology (McDowell *et al.* 2002a). In this study, we evaluated relations between tree size, $A_L : A_S$, hydraulic conductance and water flux in *Q. garryana*.

The objective of this study was to evaluate the hypothesis that 25 m tall *Q. garryana* individuals, having both greater hydraulic path length and $A_L : A_S$ than 10 m tall individuals, have lower K_L and water flux per unit leaf area (E_L) than 10 m trees. Additional objectives were (1) to assess the potential effect of reduced K_L and E_L on tree carbon gain by estimating carbon isotope discrimination in upper crown leaves and leaf photosynthetic capacity; and (2) to evaluate the effect of seasonal variation in soil moisture content on water fluxes in 10 m and 25 m trees.

Materials and methods

SITE AND SPECIES

The oak site was located in Corvallis, OR, USA (44°34′ N, 123°15′ W) at an elevation of 90 m. Mean annual temperature is 11·1 °C, and mean annual precipitation is 1100 mm. Two plots were located ≈50 m apart in adjacent oak groves. Eight trees in each of the two plots were selected for sap flow and biometric measurements. *Quercus garryana* trees comprised >99% of total plot basal area, and all of the canopy leaf area, in each plot. Further details of the plots are given in Table 1. The understorey was composed of grass species with a few suppressed individuals of *Prunus* spp. and *Toxicodendron diversilobum* shrubs. Soils on this site are classified as a clay loam of the Joly series. Measurements in this study were conducted during the 1999 growing season.

TREE WATER FLUX AND HYDRAULIC CONDUCTANCE

Eight trees of each size class were selected for sap-flow measurements using the thermal dissipation technique (Granier 1987; Granier 1985). A total of 47 sap-flow sensors were deployed in the trees; 25 in the 25 m trees, and 22 in the 10 m trees. A combination of 10 and 20 mm long sensors was used to assess circumferential and radial variation in sap flow. We used 10 mm sensors in the outermost sapwood to minimize errors associated with longer sap-flow probes inserted across non-uniformly conducting sapwood (Phillips, Oren & Zimmermann 1996; Clearwater *et al.* 1999), which is generally the case in ring-porous oaks (Granier *et al.* 1994).

A data logger and multiplexor system (CR10x and AM416, Campbell Scientific, UT, USA) sampled (every 10 s) and averaged and recorded (every 10 min) temperature differences between heated probes and reference probes in each sensor. Probe temperature differences were converted to sap flux density (J_S, g H_2O m^{-2} sapwood s^{-1}) using an empirical equation developed by Granier (1987, 1985). J_S was scaled up to the whole tree (J; g s^{-1}) by (1) multiplying the average sap flux density of outer sapwood (0–1 cm outer band of xylem) in each plot by the area of outer sapwood for trees in that plot; (2) doing the same with inner sapwood (1–3+ cm inside the cambium of all trees); and (3) adding (1) and (2). This method of scaling of sap flux density to the canopy requires independence between J_S and tree size or sensor position on trees within each of the plots; therefore we tested for a significant relationship between these variables at each site before employing this scaling method.

Transpiration per unit leaf area (E_L; mol m^{-2} s^{-1}; see below for determination of leaf area, L) was estimated as:

$$E_L = J/L \qquad \text{eqn 2}$$

Because J is measured near the base of trees, there is generally a time lag and frequency attenuation of the transpiration signal (Phillips *et al.* 1997). To correct for this time lag we performed cross-correlation analysis between J and vapour pressure deficit of the canopy air (D) and used the time lag with the highest correlation coefficient to estimate instantaneous transpiration.

Whole-tree leaf-specific hydraulic conductance (K_L; mol m^{-2} s^{-1} MPa^{-1}) was computed as:

$$K_L = E_L/(\Psi_S - \Psi_l - \rho gh) = E_L/(\Delta\Psi_{S\text{–}l} - \rho gh) \qquad \text{eqn 3}$$

where Ψ_S and Ψ_l are soil and leaf water potential (MPa), respectively (see below for water potential measurements); ρ is the density of liquid water (1000 kg m^{-3}); g is acceleration due to gravity (9·81 m s^{-2}); and h is canopy height (10 or 25 m in this study). We approximated Ψ_S as equal to predawn Ψ_l, corrected for gravity. While the effect of gravity on Ψ_l is subtracted from the overall potential difference in equation 3, it is important to note that gravity reduces the absolute value of leaf water potential more in taller trees (with a gradient of 0·01 MPa m^{-1}), which has an independent influence on cavitation vulnerability, and constitutes a related hydraulic cost of tree height.

LEAF AND SAPWOOD AREAS

Canopy one-sided leaf area per unit ground area (L) was estimated with 1·6 m^2 leaf collectors placed in the understorey of both plots after spring leaf production. Leaves were collected during and after winter leaf fall. Leaf areas were estimated by multiplying dry weight of all oak leaves by a leaf area to dry weight ratio of fallen leaves determined for each set of trees. Leaf collectors were distributed randomly within circular boundaries, established around each plot to encompass all the study trees and any other trees that happened to lie within the circular boundaries. The 10 m trees plot (9 m radius) contained 14 leaf collectors beneath 32 trees, 30 of which were *Q. garryana*; the 25 m trees plot (15 m radius) contained 25 leaf collectors beneath 14 trees, 10 of which were *Q. garryana*. Total ground area covered by leaf area collectors encompassed 9% in the 10 m trees plot and 6% in the 25 m trees plot.

Sapwood depth was estimated visually from cores taken from at least two locations on each of the sap flow trees, at the approximate height of sap flow sensor installation. A distinct colour change indicated the boundary between sapwood and heartwood. Sapwood area (A_S) was computed from estimates of sapwood, bark depth and tree diameter. Table 1 lists average sapwood areas.

SOIL AND LEAF WATER POTENTIAL, AND ASSOCIATED ENVIRONMENTAL MEASUREMENTS

Soil water potential (Ψ_S) in the rooting zone was estimated on mid- and late summer days (2, 13 and 23 July, 16 September). Ψ_S was estimated from predawn leaf water potential (Ψ_l) measurements from oak crowns with a Scholander-type pressure chamber (PMS Instruments, OR, USA). Ψ_S was derived from predawn Ψ_l by subtracting the gravitational component of Ψ_l to correct for the height of leaves, under the assumption that Ψ_l of the trees had equilibrated with bulk Ψ_S by predawn hours. This assumption is supported by the finding that sap fluxes stabilized to near zero by predawn hours (see Appendix). Scaffolding towers were constructed to gain access to the tops of three tree crowns in each plot. On each of three trees in each plot, leaves from at least three upper canopy branches were used to measure predawn Ψ_l for estimation of Ψ_S.

Volumetric soil moisture (θ, $m^3\ m^{-3}$) was estimated on a semi-weekly basis using a time domain reflectometry (TDR) technique (Nikodem 1966; Topp & Davis 1985), with pairs of stainless steel rods 1 m in length installed vertically in five locations in each of the plots. A TDR calibration equation for clay loam was used in this study (Gray & Spies 1995). Additionally, hourly pan evaporation and rainfall data were obtained from a US Bureau of Reclamation weather station located ≈10 km from the site.

Diurnal Ψ_l measurements were made on sun-exposed leaves near crown tops. On each of the three trees in each plot, diurnal rounds of Ψ_l were made during periods representing the early to mid-season (12, 13, 23, 27, 28 July) and late season (16, 17 September). On these days, approximately every half-hour from mid-morning until late afternoon two to three leaf samples were harvested from upper branches for Ψ_l measurements. For computing K_L in equation 3, the closest half-hourly Ψ_l measurement was used in conjunction with each 10 min estimate of E_L.

Table 1. Plot and tree characteristics

Variable	25 m plot	10 m plot
Plot area (ha)	0·071	0·025
Oak tree age (years)	250	40
Oak canopy height (m)	25	10
Oak (non-oak) stem density (n ha^{-1})	140 (60)	1200 (80)
Oak diameter at 1·3 m (m)*	0·56 ± 0·05	0·23 ± 0·01
Oak (non-oak) basal area ($m^2\ ha^{-1}$)	36·3 (0·5)	23·2 (0·1)
Oak sapwood depth at mid-bole (cm)	4·2 ± 0·4	4·3 ± 0·1
Oak sapwood area ($m^2\ ha^{-1}$)	9·1	13·9
Oak leaf area index ($m^2\ m^{-2}$)	3·3 ± 0·10	3·2 ± 0·24
Oak leaf area: sapwood area ($m^2\ cm^{-2}$)*	0·37 ± 0·01	0·23 ± 0·02

Standard errors are indicated for some variables. Values in parentheses correspond to tree species other than *Quercus garryana* that occurred within plot boundaries.
*$P < 0·0001$.

LEAF CARBON ISOTOPES, PHOTOSYNTHETIC CAPACITY AND NITROGEN CONCENTRATION

To provide time-integrated indications of stomatal restrictions to crown gas exchange, foliage samples were used for determination of carbon isotope discrimination (Δ). Cellulose was extracted from foliage samples using the method described by Wise, Murphy & D'Addieco (1945). Cellulose $\delta^{13}C$ was analysed using an isotope ratio mass spectrometer at the Idaho Stable Isotope Laboratory (Moscow, ID, USA). Because foliage was extracted from ventilated, exposed branches near the top of each tree, we assumed that light availability was similar across sampling positions. Because the plots were separated by only ≈50 m, we assumed that $\delta^{13}C$ of the source air ($\delta^{13}C_a$) was similar and equal to −8·00‰ (Farquhar, Ehleringer & Hubick 1989). According to the hydraulic limitation hypothesis, values of Δ should be lower for tall *vs* smaller trees in similar environments.

Photosynthetic capacity was assessed by the measurement of photosynthetic response to intercellular CO_2 concentration (A–C_i curves), and leaf N concentration. A was measured on upper crown leaves with a gas-exchange system (Li-Cor 6400, Li-Cor, NE, USA), with cuvette [CO_2] varied in the following order: 40, 30, 20, 10, 40, 60, 80, 100, 120, 160, 200 Pa. After each exposure to a new [CO_2], 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] over a 60 s period after steady state had been reached. Five A–C_i curves were determined

on each of three 10 m trees (total of 15 A–C_i curves), and two curves were determined on each of two 25 m trees (total of four A–C_i curves). The maximum carboxylation rate and maximum electron transport rate were calculated from the A–C_i curves using non-linear least-squares regression to fit the values of these parameters to the best fit equations of von Caemmerer & Farquhar (1981) in the photosynthesis model of Harley *et al.* (1992).

Leaf N concentration was measured as a further, indirect measure of photosynthetic capacity, as photosynthetic capacity is generally highly correlated to leaf N concentration (Field & Mooney 1986; Livingston *et al.* 1998). We used foliage from gas-exchange measurements for determination of leaf [N]. Upper crown leaves were taken from three 10 m and three 25 m trees. Within each tree sampled, three leaf subsamples were collected. We determined leaf [N] on a subset of whole-foliage samples that were dried at 65 °C for 48 h, ground with a mortar and pestle, and analysed by combustion (LECO Corp., St Joseph, MI, USA). For statistical analysis, subsamples were pooled and a t-test (Systat Inc., CA, USA) was performed on three samples from each tree size class.

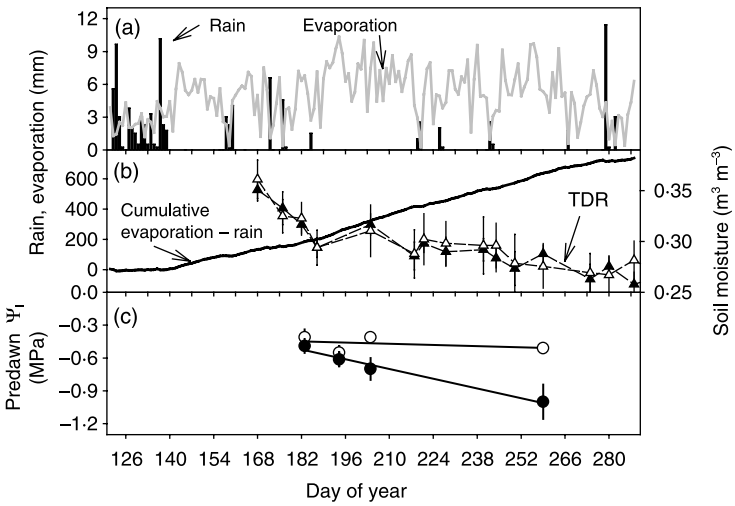

Fig. 1. (a) Rainfall and pan evaporation near the plots. (b) Cumulative evaporation minus rainfall, and soil moisture (with standard error bars) averaged from five locations under the 10 m (△) and the 25 m trees (▲) (c). Predawn leaf water potentials measured from 10 m (○) and 25 m trees (●). Standard error bars are not visible on all points.

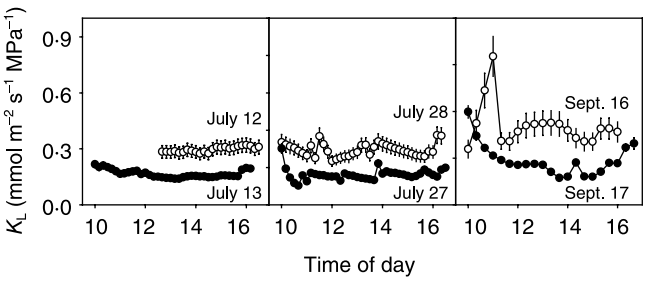

Fig. 2. Whole-tree leaf-specific hydraulic conductance (K_L, mmol m^{-2} s^{-1} MPa^{-1}) for 10 m (○) and 25 m trees (●) during three diurnal courses from mid- to late season 1999. Standard error bars are not visible on all points.

Results

SOIL MOISTURE, CLIMATE AND DEVELOPMENT OF PLANT WATER STRESS

The growing season of 1999 was abnormally dry, with only 65% of the 30-year mean rainfall for the months from May through October. The temporal distribution of precipitation over the growing season of 1999 was typical, with relatively large amounts during May and June and little during July, August and September (Fig. 1a). Water availability prior to the 1999 growing season was high (182 mm from January through April 1999, compared to the 30-year mean of 120 mm), and did not affect the timing of leaf expansion (leaf buds on 10 m and 25 m trees opened during mid-April and leaves were fully expanded by mid-May).

Beginning in June 1999, accumulated pan evaporation exceeded accumulated rainfall, and the accumulated difference increased monotonically from June through October (Fig. 1b). Soil moisture in both sites decreased sharply during June 1999, then decreased less rapidly through the rest of the growing season (Fig. 1b). We did not detect a difference in the time series of soil moisture between the two sites (Fig. 1b). However, predawn Ψ_l of 25 m trees decreased over the growing season, reaching –0·9 MPa in October, but did not decrease in 10 m trees, which averaged about –0·3 MPa throughout the growing season (Fig. 1c). Midday Ψ_l was not different between 10 m and 25 m trees, reaching approximately –3·0 MPa in both 10 m and 25 m trees (P = 0·6).

HYDRAULIC CONDUCTANCE AND WATER FLUX

Diurnal values of K_L estimated from sap flux and leaf-soil $\Delta\psi$ measurements were lower in 25 m trees than in 10 m trees. Values for K_L ranged from ≈0·1–0·5 and 0·2–0·8 mmol m^{-2} s^{-1} MPa^{-1} for 25 m and 10 m trees, respectively (Fig. 2). These values of K_L are about an order of magnitude greater than those estimated for branches of *Quercus robur* L. ssp. *robur* Kl. et Kr. et Rol. (Rust & Roloff 2002); an order of magnitude less than those estimated for whole trees of *Quercus laevis* Walt., *Quercus margaretta* Ashe and *Quercus incana* Bartr. (Donovan *et al.* 2000); and within the range of values for whole trees of *Quercus marilandica* Muenchh. and *Quercus rubra* Lam. (Reich & Hinckley 1989).

J_S and E_L were lower in 25 m trees than in 10 m trees, as shown by daily sums throughout the growing season (Fig. 3a,b). Because of greater $A_L : A_S$ in 25 m trees (Table 1), differences in E_L were more pronounced than differences in J_S (compare Fig. 3a,b). E_L of both 10 m and 25 m trees did not appear to be sensitive to soil water depletion in the top 1 m or, in 25 m trees, to predawn Ψ_l (compare Fig. 3 with Fig. 1).

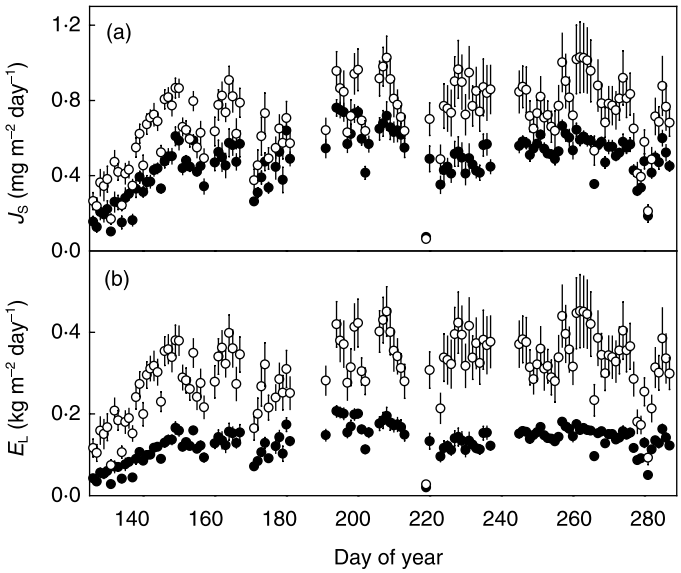

Fig. 3. (a) Whole-tree water flux per unit sapwood area (J_S, mg m^{-2} day^{-1}) in 10 m (○) and 25 m trees (●). Bars represent standard errors. J_S is the weighted average of both outer (0–10 mm beneath cambium) and inner (10–30+ mm beneath cambium) sap flux densities. (b) Whole-tree water flux per unit leaf area (E_L, kg m^{-2} day^{-1}).

There was no relationship between J_S and either tree size ($P = 0{\cdot}33$) or sensor position around the circumference of trees ($P = 0{\cdot}2$), within either of the two size classes. However, the weighted average J_S shown in Fig. 3(a) masked considerable within-tree variability in water flux. J_S of inner xylem (10–30+ mm inside cambium) was less than that of outer xylem (0–10 mm inside cambium) in both 10 m and 25 m trees. In 10 m trees, the ratio of inner-to-outer J_S was $0{\cdot}41 \pm 0{\cdot}07$, while for 25 m trees, the ratio was $0{\cdot}30 \pm 0{\cdot}13$. There was no dependence of these ratios on soil moisture variability ($P > 0{\cdot}5$) or day of year ($P > 0{\cdot}5$). 10 m trees showed a slight but significant increase in the ratio of inner to outer J_S with the magnitude of J_S ($P < 0{\cdot}0001$, $r^2 = 0{\cdot}24$), whereas 25 m trees showed no change in the ratio of inner to outer J_S with the magnitude of J_S ($P = 0{\cdot}12$).

LEAF CARBON ISOTOPES, NITROGEN, AND PHOTOSYNTHETIC CAPACITY

Carbon isotope discrimination of leaves was consistent with greater time-integrated stomatal resistance in 25 m trees compared to 10 m trees. Δ from leaves of 10 m and 25 m trees averaged 16·9 and 15·6‰, respectively ($P < 0{\cdot}0001$). The interpretation of greater stomatal resistance in 25 m trees could possibly be confounded by differences in photosynthetic capacity between 10 m and 25 m trees, as we discuss later.

Leaf N content was marginally greater ($P = 0{\cdot}10$) in 25 m trees (2·82%, 1 SE = 0·06%) compared to 10 m trees (2·66%, 1 SE = 0·06%). We did not detect a difference in either carboxylation efficiency (50·6 *vs* 41·4 μmol m^{-2} s^{-1} in 10 m [$n = 5$] and 25 m [$n = 2$] trees, respectively; $P = 0{\cdot}40$) or maximum electron transport (147·7 vs. 162·0 μmol m^{-2} s^{-1} in 10 m [$n = 3$] and 25 m [$n = 2$] trees, respectively; $P = 0{\cdot}61$).

Discussion

Whole-tree water fluxes were reduced in 25 m trees compared to 10 m trees both per unit sapwood area and per unit leaf area (Fig. 3). Because 25 m trees had $A_L : A_S$ 1·6 times that of 10 m trees (Table 1), the substantial differences in water flux per sapwood area between tree sizes were magnified further when expressed per unit leaf area (compare Fig. 3a,b). The increase in $A_L : A_S$ with tree size is opposite to that expected if $A_L : A_S$ is regulated to maintain leaf gas exchange (Becker *et al.* 2000; Cernusak & Marshall 2001). If changes in $A_L : A_S$ as trees grow in height were to compensate completely for increasing tree hydraulic resistance (to maintain leaf-level vapour conductance; McDowell *et al.* 2002b), 25 m trees would need to have $A_L : A_S$ 0·69 times that of 10 m trees, instead of the observed factor of 1·6. Thus the changes in $A_L : A_S$ with tree size observed in this study exacerbate, rather than moderate, differences in leaf gas exchange.

Substantial differences found in K_L also show evidence for a size-related hydraulic limitation to canopy gas exchange and net C gain in *Q. garryana*. K_L was substantially greater in 10 m compared to 25 m trees (Fig. 2). Moreover, we have estimated (data not presented) substantially greater growth efficiency (Waring, Thies & Muscato 1980) in 10 m trees compared to 25 m trees (0·29 *vs* 0·094 kg C m^{-2} year^{-1}, respectively; $P = 0{\cdot}0002$), which is consistent with (although not incontrovertible evidence of) a hydraulic limitation to tree growth. Finally, carbon isotope discriminations in leaves are consistent with stomatal restrictions to gas exchange in 25 m compared to 10 m oaks.

INTERRELATIONSHIP BETWEEN HYDRAULIC AND GAS-EXCHANGE VARIABLES

The hydraulic limitation hypothesis offers a plausible explanation for the linkage between hydraulic and gas-exchange variables measured in this study. Reduced K_L must cause Ψ_l to be reduced as trees become taller, for a given E_L. In this study we have observed a similar minimum Ψ_l of approximately –3·0 MPa, independent of tree size (this differs from a minimum Ψ_l that decreased with tree size in *Pseudotsuga menziesii* (McDowell *et al.* 2002b; Phillips *et al.* 2002) and *Eucalyptus saligna* (Barnard & Ryan 2003)). With reduced K_L in taller trees, a reduction in mean stomatal conductance of the canopy (G_S) is necessary to maintain a threshold minimum water potential (Bond & Kavanagh 1999; Hubbard *et al.* 2001). Having the same minimum leaf water potential independent of tree size would force a lower G_S and E_L in 25 m trees, because for a given Ψ_{S0}, K_L reduces Ψ_l more in 25 m than in 10 m trees, placing Ψ_l closer to a threshold for stomatal closure.

ADDITIONAL CONSIDERATIONS

Several factors that were not considered in detail in this study could play an important role in regulating water transport and gas exchange in trees of different size. First, we did not determine root density or volume, which could play an important role in the regulation of whole-tree water transport (Dawson 1996; Magnani, Mencuccini & Grace 2000). Second, the dynamic use of stored water could alleviate steady-state hydraulic limitations to water transport (Phillips *et al.* 2003). Third, greater sapwood conductivity (k_S) in larger trees could have compensated for hydraulic limitations of tree size. Finally, estimates of Δ may have been influenced not only by stomatal restrictions to gas exchange, but also by variation in photosynthetic capacity among tree size classes. Potential impacts of several of these factors are discussed below.

WATER STORAGE

While we observed that predawn Ψ_l was maintained in 10 m trees but continued to decrease in 25 m trees with soil moisture depletion (Fig. 1c), it is of interest that these divergent patterns of predawn water status were not mirrored by a similar divergence of soil moisture between the plots (Fig. 1b). This could indicate either an increasing resistance of the soil to root interface in 25 m trees, or a greater degree of long-term depletion of internal water stores in 25 m trees compared to 10 m trees, supporting transpiration over the growing season. Notwithstanding our analysis (see Appendix) that trees did not substantially extend night-time recharge of storage into predawn hours, in a related study at this site (Phillips *et al.* 2003) time-lag analysis between branch and bole sap flow sensors in three trees of each size class indicated that depletion of internal water storage in 25 m trees increased, as a percentage of total daily transpiration, from early to late season (from 10% in the early season to 23% in the late season in 25 m trees, compared to from 9% in the early season to 13% in the late season, for 10 m trees). A more severe seasonal depletion of water storage in the larger trees could explain the more pronounced decline in predawn Ψ_l of 25 m trees. Long-term use of stored water has been detected in conifer species by a seasonal decline in sapwood water content (Waring & Running 1978; Waring, Whitehead & Jarvis 1979), and to the extent that this water comes from cavitated vessels, it may serve to conserve soil water and promote drought tolerance (Sperry 1995; Sperry 2000).

Related to the above point, in comparing Figs 1–3 an interesting pattern emerges that requires explanation. While midday leaf water potentials were similar (approximately –3·0 MPa), the seasonal reduction in predawn Ψ_l of 25 m trees (Fig. 1) indicates a reduced leaf-to-root water potential difference in the late season in 25 m trees. Coupled with a stable seasonal maintenance of E_L observed in 25 m trees (Fig. 3), this suggests that K_L of 25 m trees must have increased in the late season. In fact, this appears to be the case, especially in the morning hours of the late season (Fig. 2, right panel). Because no significant rain fell between the mid- and late season, the apparent increase in late-season K_L is probably due to the increased use of stored water in both 25 m and 10 m trees (Phillips *et al.* 2003). Increased late-season utilization of stored water would be consistent with the especially pronounced increase of K_L observed in morning hours (Fig. 2, right panel), when withdrawal of stored water is high (Phillips *et al.* 2003). Because K_L is defined during steady-state flow conditions, dynamic contributions of stored water would represent an artefact in the K_L estimates. Nevertheless, estimates of apparent K_L that include dynamic contributions of stored water still indicate a generally lower ability for larger trees to transport water (Fig. 2, right panel).

POTENTIAL HYDRAULIC COMPENSATION DUE TO VARIATION IN k_S

Ancillary data obtained from bole increment cores suggests some compensatory changes in k_S with tree size that could moderate hydraulic constraints of tree size. Bole porosity of 25 m trees was greater than in 10 m trees [$(2{\cdot}35 \pm 0{\cdot}34) \times 10^4$ *vs* $(1{\cdot}18 \pm 0{\cdot}19) \times 10^4$ mol m^{-1} s^{-1} MPa^{-1}, respectively; $P < 0{\cdot}0001$]. However, it was apparently insufficient, and/or not representative of the entire root-to-leaf hydraulic pathway to overcome the effects of h and $A_L : A_S$ on K_L and E_L, as determined from sap flux measurements. If the above estimates of porosity can be taken to represent k_S of entire boles (assumed roughly to be 20 and 7 m for 25 m and 10 m trees, respectively), equation 1 estimates maximum bole K_L values of 0·25 and 0·51 mol m^{-2} s^{-1} MPa^{-1} for 25 m and 10 m trees, respectively. This indicates that, at least in boles, the larger k_S of 25 m trees is insufficient to overcome an overall reduction of K_L caused by larger hydraulic path length and $A_L : A_S$ in 25 m trees. These estimates of k_S provide an incomplete indication of the integrated control of tree water flux by vascular anatomy, and the degree of compensation of hydraulic limitations afforded by k_S in *Q. garryana* requires further study.

CARBON ISOTOPE DISCRIMINATION AND PHOTOSYNTHETIC CAPACITY

The reduced Δ in 25 m trees may be due to some combination of (1) lower leaf stomatal conductance (g_S), and (2) greater leaf photosynthesis (A) for a given g_S, which both reduce the ratio of intercellular to ambient [CO_2]. However, a simple equation (Goldstein *et al.* 1996) that relates Δ to A and g_S:

$$\Delta = 29 - 0{\cdot}11 \times A/g_S \qquad \text{eqn 4}$$

together with initial slopes of A/g_S from ancillary gas-exchange measurements on upper crown leaves

(unpublished data) indicate that there is probably a negligible effect on Δ of a slightly greater A/g_S in 25 m trees (19·2 and 19·1‰ in 25 m and 10 m trees, respectively). Moreover, photosynthetic capacity and leaf N of 10 m and 25 m trees were not substantially different. We conclude that the measured differences in Δ are likely to be largely due to reduced g_S in 25 m trees.

HYDRAULIC LIMITATION IN DROUGHT ADAPTED TREE SPECIES

Drought-adapted tree species such as *Q. garryana* can be viewed as providing a strong test of the hydraulic limitation hypothesis (Ryan & Yoder 1997) because tree height and drought present fundamentally similar challenges to tree function. Both factors reduce leaf and xylem water potentials, which have consequences for leaf photosynthetic function (Tezara *et al*. 1999) and vulnerability to xylem cavitation (Sperry, Alder & Eastlack 1993). Most North American oak species can tolerate or avoid drought by deep root systems and maintenance of high photosynthetic rates at low leaf water potentials (Abrams 1990; Kolb & Stone 2000), although little ecophysiological information is available for *Q. garryana* (Thilenius 1968; Krygier 1971; Hibbs & Yoder 1993). Both size classes of *Q. garryana* in this study appeared to tolerate drought by maintaining uniform E_L rates throughout the growing season (Fig. 3), even though soil moisture in the top 1 m of soil declined over the same period (Fig. 1), and predawn Ψ_l declined in 25 m trees (Fig. 1). We did not determine rooting depth, but the observed insensitivity of E_L to soil moisture in the top 1 m of soil implies deep rooting in both size classes.

Conclusion

Our results raise the question of the adaptive significance of increased $A_L : A_S$ with tree size. Such a phenomenon is counter to a relatively constant $A_L : A_S$ predicted by the pipe model (Shinosaki *et al*. 1964; Waring, Schroeder & Oren 1982; Waring 1983; Franco & Kelly 1998), or a decreasing $A_L : A_S$ with tree size predicted by West, Brown & Enquist (1999) and observed in most species. Whitehead & Jarvis (1981) hypothesized that, in closed-canopy forests, changes in $A_L : A_S$ on the tree scale accompany changes in stand density, so as to promote homeostasis in Ψ_l, L and stand transpiration. Implicit in this hypothesis is the supposition of forest homeostasis in the use of available soil water. In this study, E_L in the two plots differed substantially (Fig. 3), but L (Table 1) was similar among plots. A substantial difference in E_L between the plots without a compensating difference in L indicates substantial differences, and therefore a lack of homeostasis, in stand transpiration rate. Yet evapotranspiration appears similar from soil moisture depletion (Fig. 1; note that cumulative pan evaporation greatly exceeds rainfall and therefore soil drainage or runoff was minimal), indicating that understorey and soil evapotranspiration may compensate for differences in canopy transpiration. The results from this study may thus be consistent with the homeostatic water-use hypothesis of Whitehead & Jarvis (1981) to the extent that this hypothesis includes consideration of both canopy and understorey components (Roberts 1983; Phillips & Oren 2001). At the same time, these results provide further support and generality to the hypothesis of hydraulic limitations to tree water flux, and show that limitations to water flux are not necessarily accompanied by the structural compensation of reduced crown leaf area in larger trees.

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Appendix

STABILITY OF NIGHT-TIME TEMPERATURE BASELINES FOR SAP FLUX MEASUREMENTS

While Granier's calibration equation (Granier 1985) has previously been validated in ring-porous oaks (Granier 1985; Granier *et al*. 1994), the application of this equation depends on proper identification of zero flow baseline temperature differences between heated and reference probes (Burgess, Adams & Melby 2000). Either night-time transpiration or night-time refilling of hydraulic capacitance in trees can lead to non-zero sap fluxes during predawn hours that reduce night-time temperature differences below their zero flow value. To assess this effect, an analysis was conducted of the likelihood of substantial sap fluxes through predawn hours due to capacitance. For this analysis, the most pronounced occurrence of night-time sap flow was expected to occur in the largest trees, after a day of high evaporative demand and zero night-time evaporative demand. Therefore, on a clear day with high daytime vapour pressure deficit that approached zero during night-time hours (27–28 July 1999) we fitted exponential saturation curves to the tailing portions of diurnal temperature difference time series in the three 25 m trees equipped with five sap flow sensors each. Maximum observed temperature differences at predawn were compared to the maximum temperature differences predicted from the exponential saturation model. Average differences between observed and modelled temperature differences were small (0·35 °C, SE = 0·09 °C), and differences in peak flow rates from assuming observed *vs* modelled baseline values averaged 3·7%. In these most favourable conditions for night-time sap flow due to capacitance, these results indicated that temperature differences generally stabilized to a nearly constant level, and thus adequately represented a zero flow condition.