Effects of height on treetop transpiration and stomatal conductance in coast redwood (*Sequoia sempervirens*)

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Summary Treetops become increasingly constrained by gravity-induced water stress as they approach maximum height. Here we examine the effects of height on seasonal and diurnal sap flow dynamics at the tops of 12 unsuppressed *Sequoia sempervirens* (D. Don) Endl. (coast redwood) trees 68–113 m tall during one growing season. Average treetop sap velocity (V_S), transpiration per unit leaf area (E_L) and stomatal conductance per unit leaf area (G_S) significantly decreased with increasing height. These differences in sap flow were associated with an unexpected decrease in treetop sapwood area-to-leaf area ratios (A_S:A_L) in the tallest trees. Both E_L and G_S declined as soil moisture decreased and vapor pressure deficit (D) increased throughout the growing season with a greater decline in shorter trees. Under high soil moisture and light conditions, reference G_S (G_{Sref}; G_S at $D = 1$ kPa) and sensitivity of G_S to D ($-\delta$; $dG_S/d\ln D$) significantly decreased with increasing height. The close relationship we observed between G_{Sref} and $-\delta$ is consistent with the role of stomata in regulating E_L and leaf water potential (Ψ_L). Our results confirm that increasing tree height reduces gas exchange of treetop foliage and thereby contributes to lower carbon assimilation and height growth rates as *S. sempervirens* approaches maximum height.

Keywords: climate change, hydraulic limitation, sapflow, tree water use, water potential.

Introduction

As trees get taller and hydraulic pathways become longer, water supply to upper crown foliage becomes increasingly restricted, leading to a reduction in leaf-specific hydraulic conductance (k_L (mol m^{-2} s^{-1} MPa^{-1}); Ryan and Yoder 1997, Ryan et al. 2006). In trees with leaves that are well coupled to the atmosphere (i.e., when leaf temperature is equal to air temperature) and when water storage is negligible, the effects of reduced k_L can be examined using a simple hydraulic model for steady-state water flux through trees (Richter 1973, Jarvis 1975, Tyree and Ewers 1991, Whitehead 1998),

$$E_L = k_L \cdot (\Psi_S - \Psi_L - \rho g h) \qquad (1)$$

where E_L is transpiration per unit leaf area (mol m^{-2} s^{-1}), Ψ_S is bulk soil water potential (MPa), Ψ_L is leaf water potential (MPa) and $\rho g h$ is the gravitational pull (g) on a water column of density ρ (0.0098 MPa m^{-1}) at height h (m). The influence of gravity on water potential persists whether or not water is moving through the xylem, whereas hydraulic effects resulting from increasing friction with longer path lengths become manifest during transpiration. Within this framework, k_L may be expressed in terms of the physical properties of the conducting system,

$$k_L = K_S \cdot \frac{A_S}{A_L} \cdot \frac{1}{h} \qquad (2)$$

where K_S is sapwood-specific hydraulic conductivity (mol m^{-1} s^{-1} MPa^{-1}), A_S is sapwood area (m^2) and A_L is leaf area (m^2). The stomatal response to changes in hydraulic architecture can be evaluated using Equation 1 by substituting crown-level average stomatal conductance (G_S, mol m^{-2} s^{-1}) and air saturation vapor pressure deficit (D, MPa MPa^{-1}) for E_L,

$$G_S = \frac{k_L \cdot (\Psi_S - \Psi_L - \rho g h)}{D} \qquad (3)$$

Under steady-state conditions, Eqs. (1–3) predict that for a given height and water potential difference between soil and leaf (i.e., $\Delta\Psi_{S-L}$), G_S is proportional to k_L and inversely proportional to D. With no change in either A_S:A_L or $\Delta\Psi_{S-L}$, G_S declines in inverse proportion to height. Therefore, in species that regulate G_S to maintain Ψ_L above a minimum threshold,

tall trees with lower k_L will tend to close stomata at a lower D than short trees with higher k_L in the absence of other compensating factors. Stomatal regulation of Ψ_L appears important for protecting the vascular system from excessive damage due to embolism and to prevent dehydration of living tissues (Tyree and Sperry 1988, Jones and Sutherland 1991). Stomatal closure limits water loss and prevents Ψ_L from falling below critical levels but also restricts the diffusion of CO_2 into the leaf, thereby reducing net photosynthesis. Reductions in stomatal or crown conductance with increasing tree size and age associated with decreasing k_L (Yoder et al. 1994, Hubbard et al. 1999, Ryan et al. 2000, Schäfer et al. 2000, Delzon et al. 2004) are consistent with predictions of Eq. (3). Structural and physiological adjustments in tree hydraulic architecture can compensate for greater restrictions to water flow in taller trees, including increased $A_S{:}A_L$, increased K_S, increased capacitance or water storage, lower minimum Ψ_L and tapering of xylem conduits (Andrade et al. 1998, Becker et al. 2000, McDowell et al. 2002a, Barnard and Ryan 2003, Phillips et al. 2003, Zaehle 2005, Addington et al. 2006, Burgess et al. 2006, Scholz et al. 2007, Ambrose et al. 2009, Hölttä et al. 2009). Such adjustments are common but not always consistent among species or sites and are often insufficient to completely offset reductions in k_L due to increasing height (Ryan et al. 2006). In addition, the cost associated with such compensating mechanisms needs consideration. For example, a decrease in minimum Ψ_L thresholds with height could compensate for decreased k_L but may result in increased risk of embolism and loss of the conducting system. More negative thresholds with increasing height have been reported in several species, including *Pseudotsuga menziesii* (Phillips et al. 2002, McDowell et al. 2002a), *Pinus contorta* (Yoder et al. 1994) and *Eucalyptus saligna* (Barnard and Ryan 2003), but not in others such as *Pinus ponderosa* (Yoder et al. 1994, Hubbard et al. 1999, Ryan et al. 2000). Regardless of whether such adjustments occur, changes in structural and physiological traits regulating water flux appear to be closely coordinated in a manner consistent with the simple model linking G_S to tree hydraulic properties expressed in Eq. (3) (Ryan et al. 2006).

Stomata typically close in response to an increase in D, apparently as a means by which plants can minimize water loss while simultaneously maximizing carbon gain (Cowan 1977, Franks 2004). Despite widespread observations of stomatal responses to humidity (expressed as either relative humidity or D), there is still no consensus on the mechanism driving this response (Meinzer 2002, Franks 2004, Buckley 2005). Some evidence suggests that stomatal closure with increasing D occurs as a feedback response to E_L and water loss rather than as a direct response to humidity (Mott and Parkhurst 1991, Monteith 1995). However, other studies suggest a strong direct stomatal response to changes in humidity (e.g., Kerstiens 1997, Buckley and Mott 2002, Shope et al. 2008). The magnitude or slope of the decline in stomatal conductance (g_s) for a given change in D reflects the sensitivity of the response (Oren et al. 1999). As predicted by Eq. (3), observations across a wide range of species and ecosystems show that stomatal sensitivity to D is proportional to maximum g_S or G_S (Sanford and Jarvis 1986, Yong et al. 1997, Oren et al. 1999, Ewers et al. 2000, 2005, Schäfer et al. 2000, Addington et al. 2004, 2006). Given the proportional relationship between k_L and G_S, it follows that trees with high k_L should have high G_S and therefore a greater sensitivity to changing D. Consistent with this prediction, both g_S and stomatal sensitivity to changing soil and atmospheric moisture decreased with increasing height in *P. menziesii* trees, leading to large differences in g_S among height classes during wet and mild conditions and minor differences during drought (McDowell et al. 2005). Thus, in species that adjust g_S to regulate minimum Ψ_L, differences in environmental sensitivity among different-sized trees appear to alter the timing and degree of hydraulic limitations to gas exchange.

While much progress has been made over the last several decades in examining tree height effects on water transport and gas exchange, it has not been possible to assess fully the biophysical constraints to these processes because most relevant studies have been either restricted to short-term measurements or conducted in trees less than half of the maximum-recorded height of a species (Ryan et al. 2006). Because the effects of gravity are directly related to absolute height and not just the range of heights investigated, important insights into hydrostatic constraints on tree performance may be gained through examination of trees approaching their maximum known height. In this study, we examined the effects of height on treetop E_L and G_S over the course of an entire growing season in *Sequoia sempervirens* (D. Don.) Endl. (coast redwood) trees ranging from 59 to 98% of maximum known tree height. We compared sap flow dynamics at the tops of trees of different heights in order to isolate height-related effects without the confounding influence of within-crown microclimate gradients. Instantaneous leaf gas exchange measurements and bulk leaf stable carbon isotope ratios (δ^{13}C) in *S. sempervirens* provide evidence of greater stomatal limitation of photosynthesis with increasing height (Koch et al. 2004, Ishii et al. 2008, Ambrose et al. 2009, Mullin et al. 2009). We therefore hypothesized that treetop E_L and G_S in *S. sempervirens* would decrease with increasing height regardless of any potential compensating structural or physiological adjustments. Because of the proportional relationship that exists between k_L and G_S, we further hypothesized that G_S sensitivity to D would decrease with increasing height, leading to greater differences in E_L and G_S among *S. sempervirens* trees of different heights during the wet season than during the dry season.

Materials and methods

Site description

This study was conducted in 2008 at Humboldt Redwoods State Park (HRSP) in northern California (40°20′ N, 124°0′ W, between 30 and 50 m above sea level). Study trees were located on the floodplain of Bull Creek within an old-growth forest

dominated by *S. sempervirens*. Annual precipitation at HRSP ranges from 1524 to 2032 mm with most rainfall occurring in the winter and fog occurring throughout the year (California State Parks). We selected 12 trees in three height classes (hereafter referred to as the 72-, 94- and 111-m height classes) spanning a 45-m height gradient for examination (Table 1). All trees were accessed using rope-climbing techniques. To minimize confounding effects of differing microclimates on height-related trends in sap flow dynamics, we selected trees with fully exposed upper crowns that were not overtopped by adjacent trees. We obtained and analyzed digital hemispherical photographs to test whether light availability was similar at the top of each tree (WinScanopy, Régent Instruments Inc.). These analyses revealed that Total Site Factor, the relative amount of incident total radiation (direct + diffuse) received at each treetop during the growing season (Anderson 1964), did not significantly differ among height classes (Tukey–Kramer honestly significant difference (HSD), $\alpha = 0.05$), averaging 99.9 ± 0.2, 99.7 ± 0.1 and $96.6 \pm 1.5\%$ (mean $\pm$ 1 SE) for the 111-, 94- and 72-m height classes, respectively. Thus, for the purposes of this study, we considered the top of each tree to have a similar light environment.

Environmental measurements

Environmental conditions were continuously monitored at each treetop using automated solar-powered measurement systems (ICT International Ltd, Armidale, NSW, Australia). Each system logged relative humidity (RH, %), air temperature (T_a, °C), wind speed (u, m s^{-1}), photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) and leaf wetness (LW, %), and six of the systems also logged total treetop rain (mm), every 30 min. The Tetens formula (Buck 1981) was used to calculate vapor pressure deficit (D, kPa) from T_a and RH. Additional battery-powered custom-built logging systems ('WISARDS'; Northern Arizona University, Flagstaff, AZ, USA) monitored soil volumetric water content (θ, m^3 m^{-3}) every hour using dielectric soil moisture probes (ECH$_2$O probes, Decagon Devices, Inc., Pullman, WA, USA) installed from the soil surface to 15 cm depth at two locations near the base of each tree. The soil moisture probes were laboratory-calibrated for the soils at this particular site. Treetop environmental conditions and soil moisture in the upper rooting zone did not significantly differ among tree height classes. Therefore, the mean value of all 12 trees for each environmental variable at each time period was used in our analyses.

Sap flow measurements

Sap flow was continuously monitored in the main trunk near the top of each study tree using the Heat Ratio Method (HRM; Burgess et al. 2001). Treetops were defined as orthotropic stems, branches and foliage above 90% of the total height of each tree. Mean treetop length (i.e., total height − HRM probeset height) was 4.7 ± 1.1 m ($\pm$ 1 SE) and did not significantly differ with tree height. Depending upon trunk diameter, two or three replicate HRM probesets connected to the main datalogger (ICT International Ltd, Armidale, NSW, Australia), each capable of measuring sap velocity at two radial depths (1.25 and 2.75 cm), were installed at approximately equal distances around the circumference of each trunk. The HRM measures the ratio of the increase in temperature, following the release of a heat pulse, at two points equidistant downstream and upstream from a line heater. Heat pulse velocity (V_h, cm h^{-1}) is calculated as (Marshall 1958),

$$V_h = \frac{k}{x} ln(v_1/v_2)3600 \qquad (4)$$

where k is thermal diffusivity of wet (fresh) wood, x is the distance (cm) between the heater and either temperature probe, and v_1 and v_2 are increases in temperature (from initial temperatures) at equidistant points downstream and upstream, respectively, x cm from the heater. The probe positions relative to the heater used with the HRM are −0.6 and 0.6 cm, hence $x = 0.6$ cm. Thermal diffusivity (k) was assigned a nominal value of 2.5×10^{-3} cm^2 s^{-1} (Marshall 1958) during measurements and was resolved empirically at a later date once sapwood properties were measured (see below).

Table 1. Summary of study tree characteristics (from Sillett et al. 2010). Values are means for each class with 1 SE of the mean in parentheses. Letters indicate significant differences at $\alpha = 0.05$.

	Height class		
	72 m	94 m	111 m
Height (m)	72.0 (1.6)[a]	94.2 (1.2)[b]	111.0 (1.1)c
DBH (cm)	185.3 (11.2)[a]	259.5 (28.8)[a]	423.0 (61.4)[b]
Wood volume (m^3)	42.6 (5.0)[a]	118.6 (22.8)[a]	358.8 (78.8)[b]
Leaf area (m^2)	1077.0 (164.4)[a]	1601.5 (256.9)[a]	3722.0 (826.3)[b]
Tree base A_S:A_L (cm^2 m^{-2})	2.59 (0.17)[a]	2.99 (0.69)[a]	2.25 (0.40)[a]
Crown base A_S:A_L (cm^2 m^{-2})	1.53 (0.14)[a]	1.64 (0.25)[a]	1.27 (0.19)[a]
Treetop A_S:A_L (cm^2 m^{-2})	6.60 (0.60)[a]	3.18 (0.49)[b]	2.15 (0.08)[b]
Treetop diameter (cm)	12.90 (0.94)[a]	17.30 (3.35)[a]	24.24 (6.03)[a]
Treetop bark depth (cm)	0.80 (0.23)[a]	1.00 (0.02)[a]	1.25 (0.42)[a]
Treetop sapwood depth (cm)	4.36 (0.42)[a]	4.12 (0.09)[a]	3.99 (0.42)[a]

DBH, diameter at breast height.

A reference velocity (i.e., $V_h = 0$) was established to correct for small errors associated with inaccurate probe spacing. The most effective method for establishing this reference velocity is to sever the xylem immediately above and below the site of probe installations to stop sap flow and obtain additional measurements after this point. However, this method causes extensive physical damage and can represent a significant impact at the treetop. An alternative non-destructive yet satisfactory method is to identify and analyze sap flow data under conditions when flow rates are assumed to be zero. Environmental conditions previously identified for *S. sempervirens* that meet this criterion are humid (>94% RH) and still pre-dawn periods (0300–0600 h) when leaves are not wet (Burgess and Dawson 2004). To prevent unacceptable damage to the study trees, we therefore adopted this method, using rain, RH and LW measurements to establish $V_h = 0$ for each HRM probeset and correcting the remaining data according to the procedures outlined in Burgess et al. (2001). Because installing sensors in xylem tissue causes mechanical damage that interrupts flow pathways and causes a wound response in the immediate vicinity of the sensors (Barrett et al. 1995), V_h data were corrected using a numerical model developed for the HRM (Burgess et al. 2001),

$$V_c = bV_h + cV_h^2 + dV_h^3 \tag{5}$$

where V_c is corrected heat pulse velocity (cm h^{-1}), and b, c and d are correction coefficients determined for a 0.17-cm wound with a −0.6, 0, 0.6 cm probe configuration.

After correcting for spacing and wound errors, sap velocity (V_s; cm h^{-1}) was determined by measuring fractions of sap and wood in xylem and accounting for their differing densities and specific heat capacities as (Barrett et al. 1995, after Marshall 1958),

$$V_s = \frac{V_c \rho_b (c_w + m_c c_s)}{\rho_s c_s} \tag{6}$$

where ρ_b is the basic density of wood [dry weight (g)/fresh volume (cm^3)], c_w and c_s are specific heat capacity of the wood matrix [1200 J kg^{-1} °C^{-1} at 20 °C (Becker and Edwards 1999)] and sap [water, 4182 J kg^{-1} °C^{-1} at 20 °C (Lide 1992)], respectively, m_c is water content of sapwood (kg), and ρ_s is the density of water (kg m^{-3}). Wood properties were determined from cores collected from near the top of each tree at the same height as the HRM sensors during wet (November) and dry (September) seasons using a 5-mm-diameter increment borer. In the laboratory, the heartwood boundary of each core was visually identified and sapwood depth measured using digital calipers. Sapwood mass was recorded to the nearest 0.0001 g. Sapwood core volumes were determined by measuring the amount of distilled water displaced by submerged cores and applying Archimedes' principle. Sapwood cores were then oven-dried at 60 °C for 2 days, and dry masses were recorded to the nearest 0.0001 g. The fresh mass, dry mass and fresh volume of each sapwood core were used to calculate ρ_b, m_c and the true value of k using the equations supplied by Burgess et al. (2001).

Sapwood cross-sectional area (m^2) of treetops was determined using measurements of trunk diameter, bark depth and sapwood depth at each HRM probeset location (Table 1). Total sapwood area was divided into concentric annuli delimited by the midpoint between HRM measurement depths. Volumetric sap flow (Q, g h^{-1}) was calculated by multiplying the mean V_s of all replicate HRM sensors at each measurement depth and the cross-sectional area of conducting sapwood within the corresponding sapwood annulus and then summing these flows (Hatton et al. 1990). In this way, point estimates of V_s were weighted according to the amount of conducting sapwood in the annuli they sampled. The two HRM measurement junctions effectively sampled 81–100% of the total sapwood cross-sectional area (mean = 88.5%) in each treetop. Because there were no significant trends in treetop sap velocity with radial depth ($R^2 = 0.01$, $P = 0.58$), we applied the average measured velocity of both junctions to any remaining unsampled sapwood area. Our sampling and measurement protocol thus accounted for both radial and circumferential variation in sap flow within each treetop. Sap flow measurements were recorded every 30 min to correspond to measured environmental variables.

Calculation of E_L and G_S

Treetop transpiration per unit leaf area (E_L, g m^{-2} s^{-1}) was estimated by dividing Q by total treetop leaf area (A_L, m^2) distal to the point of measurement. Leaf area was provided by a companion study examining the structure and growth of the same trees (Sillett et al. 2010). To estimate E_L from Q, water capacitance within the tree above the point of measurement was assumed to be negligible due to the small trunk wood volumes and short lengths of the treetops. To test this assumption, capacitance was analyzed using an approach that examines whether the correlation of Q with D is stronger for current D or for some prior time period (Phillips et al. 1997). If capacitance affects transpiration, the correlation of Q and D will be greater for some earlier time than for current D. For all trees, the correlation of Q and current D was greater than the correlation of Q and any D prior to measurement of Q. Therefore, capacitance effects on Q were determined to be negligible at the time scale of our measurements, and no time-lag adjustments were deemed necessary. To further ensure that time lags due to the effects of hydraulic capacitance and resistance did not influence our results, daily mean E_L (mmol m^{-2} s^{-1}) values for each tree were calculated from 0500 to 0500 h (Phillips and Oren 1998). After converting D into partial pressure units (kPa kPa^{-1}), treetop average stomatal conductance to water vapor (G_S, mmol m^{-2} s^{-1}) was estimated as

$$G_S = \frac{E_L}{D}. \tag{7}$$

This equation assumes that D is close to the leaf-to-air vapor pressure deficit [i.e., boundary layer conductance

$(g_b) \gg$ stomatal conductance (g_s)]. This assumption is generally valid for well-coupled trees such as conifers (Jarvis and McNaughton 1986) and is likely to be true in this study because of the very small, scale-like leaves and exposed nature of the treetops. To test this assumption, we examined the magnitude of the influence of wind speed (u) on the relationship between Q and D at high light $(I_P > 1000$ μmol m^{-2} s^{-1}). We compared Q during periods of high wind $(u \geq 2.5$ m s$^{-1})$ and low wind $(u < 2.5$ m s$^{-1})$, reasoning that if $g_b \gg g_s$, the difference in Q at low versus high u would be small (Barnard and Ryan 2003). This analysis showed no difference in the relationship between Q and D at low versus high u, supporting the hypothesis that treetop foliage was well coupled to the atmosphere and that D was the primary driving force for Q. Equation 7 also assumes that there is no vertical gradient in D through the canopy for which G_S is estimated. While large vertical gradients in D have been measured throughout entire *S. sempervirens* forest canopies (Ambrose and Sillett, unpublished data), our study was focused on the well-mixed treetops where no such gradient exists. Daily mean E_L and daily mean D values were used to calculate daily mean G_S for each tree (Phillips and Oren 1998). The effects of increasing soil and atmospheric drought on diurnal patterns of E_L and G_S were examined by bin-averaging individual tree measurements within each height class every 30 min on sunny, rain-free days during wet (May; $n = 14$ days) and dry (September; $n = 17$ days) periods with similar RH, T_a and D patterns and with midday PAR values exceeding 1800 μmol m^{-2} s^{-1}. For this analysis, we removed 30-min G_S measurements when $D < 0.1$ kPa and all days with <12 values for G_S after applying the first criterion, following the approach of Phillips and Oren (1998). Soil volumetric water content on these sample days was 0.25 ± 0.01 m^3 m^{-3} in the wet period and 0.16 ± 0.00 m^3 m^{-3} in the dry period (mean ± SD).

Response of G_S to D

In trees with well-coupled foliage, variation in D is often the largest determinant of Gs (Jarvis and McNaughton 1986). By carefully partitioning data into categories of soil moisture and light and performing a boundary line analysis on G_S versus D within each category, correlations between driving variables can be removed, and the response of G_S to D can be isolated and analyzed (Rayment et al. 2000, Schäfer et al. 2000). In order to account for seasonal differences in θ, we performed a separate boundary line analysis on data for each tree during wet (May–April) and dry (August–September) periods of the growing season. Within each period, we partitioned the data into five light (PAR) classes: 0–499, 500–999, 1000–1499, 1500–1999 and >2000 μmol m^{-2} s^{-1}. Data within each PAR class were then subjected to a boundary line analysis designed to select data representing maximum G_S along the range of D. The upper boundary line was derived by (i) partitioning the data into 0.2 kPa D intervals, (ii) calculating the mean and standard deviation of G_S in each interval, (iii) re-

moving outliers identified by examining outlier box plots and (iv) selecting the data falling above the mean plus one standard deviation of G_S (Granier et al. 1996, Schäfer et al. 2000, Ewers et al. 2001, 2005, Addington et al. 2006). When a boundary line analysis is made on the entire data set of each tree in this manner, it allows analysis of the best physiological response under measured conditions (Martin et al. 1997), which in this case corresponds to the highest G_S at any given D under different soil moisture and light levels (hereafter referred to as G_S'). The resulting data were then fitted to the following functional form (Oren et al. 1999),

$$G_S = G_{Sref} - \delta \cdot lnD \qquad (8)$$

where G_{Sref} is a reference G_S (defined as G_S at 1 kPa D), and $-\delta$ is the sensitivity of the G_S response to lnD [i.e., the slope of G_S versus lnD $(-dG_S/dlnD)$]. The range of D used in this analysis was 0.1–5.6 kPa.

Statistical analysis

Differences in daily V_S, E_L and G_S among height classes were examined with repeated measures analysis of variance using the Restricted Maximum Likelihood (REML) method for fitting mixed models. Height class means were compared using the Tukey–Kramer HSD test with $\alpha = 0.05$. Relationships of daytime E_L and G_S with daytime D were analyzed with nonlinear regression using a modified Gauss–Newton method with maximal 60 iterations. Relationships of daytime E_L with PAR, G_{Sref} and $-\delta$ with height and each other were analyzed using ordinary least squares regression. All statistical analyses were performed with JMP (version 8.0, SAS Institute, Cary, NC, USA). Individual trees were the units of replication.

Results

Seasonal patterns in environmental conditions

The study site experienced a cool, wet spring and fall and a warmer, drier summer characteristic of Mediterranean climates (Figure 1). During the study period, mean daytime RH was 64.4%, mean daytime T_a was 16.1 °C, mean daytime D was 0.86 kPa, mean daytime PAR was 1046 μmol m^{-2} s^{-1}, mean daytime u was 3.1 m s^{-1}, mean daytime LW was 4.9%, and mean soil θ was 0.22 m^3 m^{-3}. Total rainfall was approximately 235 mm with most rain occurring in the spring and additional smaller amounts in the fall. Soil θ closely followed rainfall patterns, rapidly increasing during rain events and exhibiting a prolonged drying trend throughout the summer. Photosynthetically active radiation reached a maximum in the middle of the summer (June–July). Daytime vapor pressure deficit (D) was lowest during the spring and fall and gradually increased through the summer, although short periods of very high D occurred throughout the study. Daytime wind speed was generally higher during the summer and tended to be highest immediately before or after large rain events. Daytime LW was highest in the spring and fall, pri-
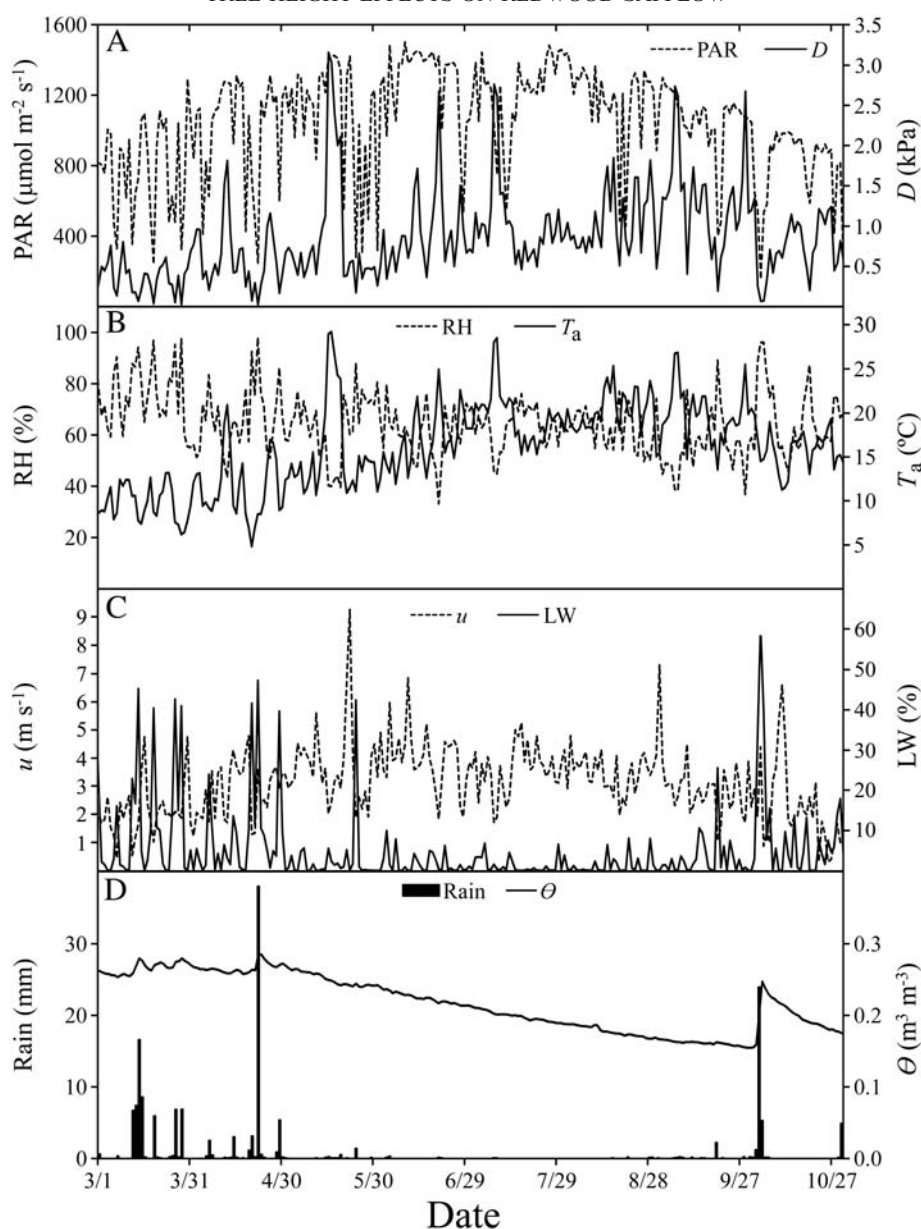
Figure 1. Mean daytime treetop environmental conditions for 12 *S. sempervirens* trees in three height classes throughout the 2008 growing season, (A) photosynthetic photon flux density (PAR) and vapor pressure deficit (D), (B) relative humidity (RH) and air temperature (T_a), (C) wind speed (u) and leaf wetness (LW), (D) rain and soil volumetric water content (θ).

marily due to the high frequency of rain events in these seasons. There were no discernable seasonal trends in daytime LW resulting from fog or dew deposition during rain-free days (data not shown). Note that Figure 1 is only intended to illustrate trends in mean daytime environmental conditions during the study and does not reflect the true magnitude of variation in these conditions. For example, although the maximum value of mean daytime PAR shown in Figure 1 is 1502 μmol m^{-2} s^{-1}, 15% of all daytime PAR measurements exceeded 2000 μmol m^{-2} s^{-1}, and 88 days (36%) of the study period experienced PAR > 2000 μmol m^{-2} s^{-1} for three consecutive hours or longer. Similarly, although the maximum value of mean daytime D in Figure 1 is 3.2 kPa, the maximum 30-min measurement of D during the study was 5.6 kPa.

Seasonal patterns in E_L and G_S

Patterns in daily treetop E_L and G_S closely followed changing site environmental conditions throughout the growing season (Figures 1 and 2). Daily mean E_L rates were highest in the middle of the summer in all height classes when PAR and D were at maximum (Figure 2A). In contrast, daily mean G_S rates were highest in the early spring in all height classes, gradually declining through the season as D increased and soil θ decreased (Figure 2B). Substantial short-term increases in E_L and decreases in G_S were also associated with spikes in daily D (e.g., 14–19 May and 21–22 June). Differences in daily E_L and G_S among height classes were highly significant ($P < 0.0001$) with declining E_L and G_S as height increased

(Figure 2, Table 2). These differences were associated with significantly lower treetop $A_S{:}A_L$ across all height classes ($P < 0.0001$, Table 1) as well as significantly lower daily treetop V_s in the 111-m compared with the 94- or 72-m height classes ($P < 0.0001$, Table 2). The largest differences in daily E_L among height classes occurred in the middle of the summer (June–July), while the largest differences in daily G_S among height classes occurred during the early spring (March–April). Seasonal and day-to-day variation in daily E_L and G_S was greater in shorter trees than taller trees. The magnitude of short-term increases in daily E_L in response to high D was greater in the spring and late fall after rain events than in the summer when soil moisture levels were lower.

Diurnal patterns in E_L and G_S during wet and dry seasons

Diurnal patterns in air RH, T_a, D and PAR were similar during sunny, rain-free days in the wet and dry seasons, with slightly lower mid-day RH and PAR and slightly higher mid-day T_a and D in the dry season (Figure 3). Air RH and T_a followed opposite diurnal patterns, while D generally followed the same diurnal pattern displayed by PAR but with a time lag. Differences in diurnal E_L and G_S were significant among height classes during both seasons, and both variables decreased with increasing height ($P < 0.0001$ for E_L and G_S in both seasons, Figure 4, Table 3). E_L rates peaked mid-day (1400–1630 h), whereas maximum G_S occurred earlier in the day (0930–1230 h) and declined thereafter (Figure 4). A distinct bi-modal pattern in G_S was observed with a mid-day depression fol-

Table 2. Mean daytime treetop sap velocity (V_s), daytime treetop transpiration (E_L), daytime treetop stomatal conductance (G_S), reference treetop G_S at $D = 1$ kPa (G_{Sref}) and sensitivity of treetop changes in D ($-\delta$; $dG_S/d\ln D$) in three *S. sempervirens* height classes ($n = 4$ trees/class). Values are means for each class with 1 SE of the mean in parentheses. Letters indicate significant differences at $\alpha = 0.05$.

	Height class		
	72 m	94 m	111 m
V_s (cm h^{-1})	4.1 (0.1)[a]	4.1 (0.1)[a]	2.0 (0.0)[b]
E_L (mmol m^{-2} s^{-1})	0.39 (0.00)[a]	0.19 (0.00)[b]	0.06 (0.00)[c]
G_S (mmol m^{-2} s^{-1})	90.8 (1.6)[a]	44.3 (0.8)[b]	13.3 (0.3)[c]
G_{Sref} (mmol m^{-2} s^{-1})	143.1 (7.9)[a]	65.4 (10.2)[b]	23.7 (6.0)[c]
$-\delta$ (mmol m^{-2} s^{-1} kPa^{-1})	87.4 (5.3)[a]	41.2 (6.9)[b]	13.3 (2.5)[c]

lowed by a slight recovery in all height classes, particularly in the wet season and in the 72- and 92-m height classes. Shorter trees showed greater differences between mean wet and dry season E_L and G_S rates than taller trees (Table 3).

Response of E_L and G_S to environmental conditions

Daytime means of E_L were significantly correlated with mean daytime D and PAR in all height classes ($P < 0.0001$ for both variables, Figure 5A and B, Table 4), while daytime G_S was only significantly correlated with mean daytime D ($P < 0.0001$, Figure 5C and D, Table 4). Both E_L and G_S exhibited non-linear responses to D, while E_L exhibited a linear response to PAR. Shorter trees had higher E_L and G_S at a given D and
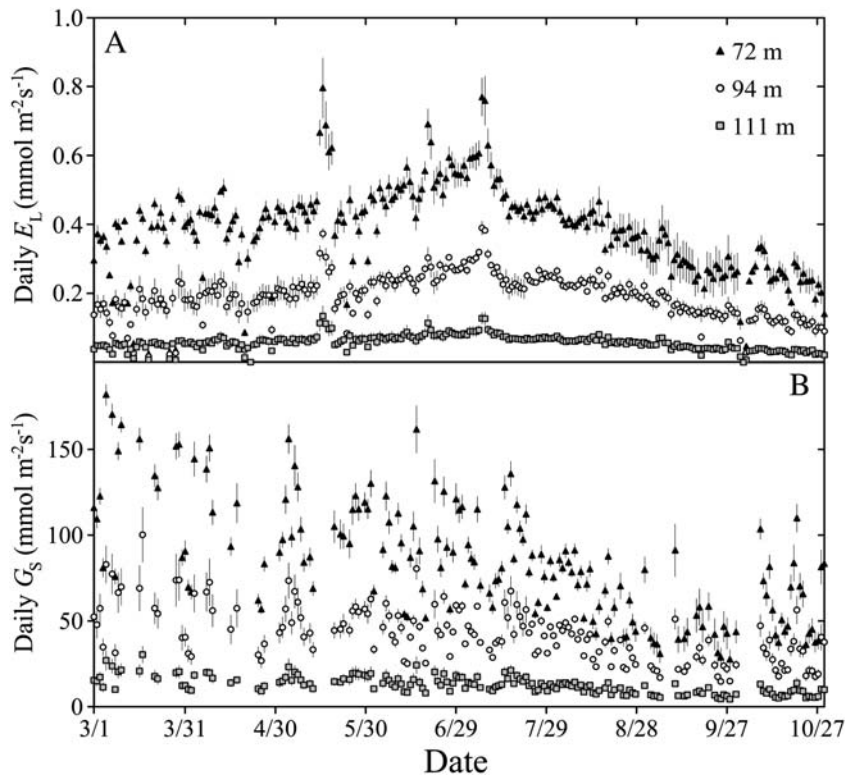

Figure 2. (A) Daily mean treetop transpiration (E_L) and (B) daily mean treetop stomatal conductance (G_S) in three *S. sempervirens* height classes (mean ± 1 SE) during the 2008 growing season ($n = 4$ trees/class).
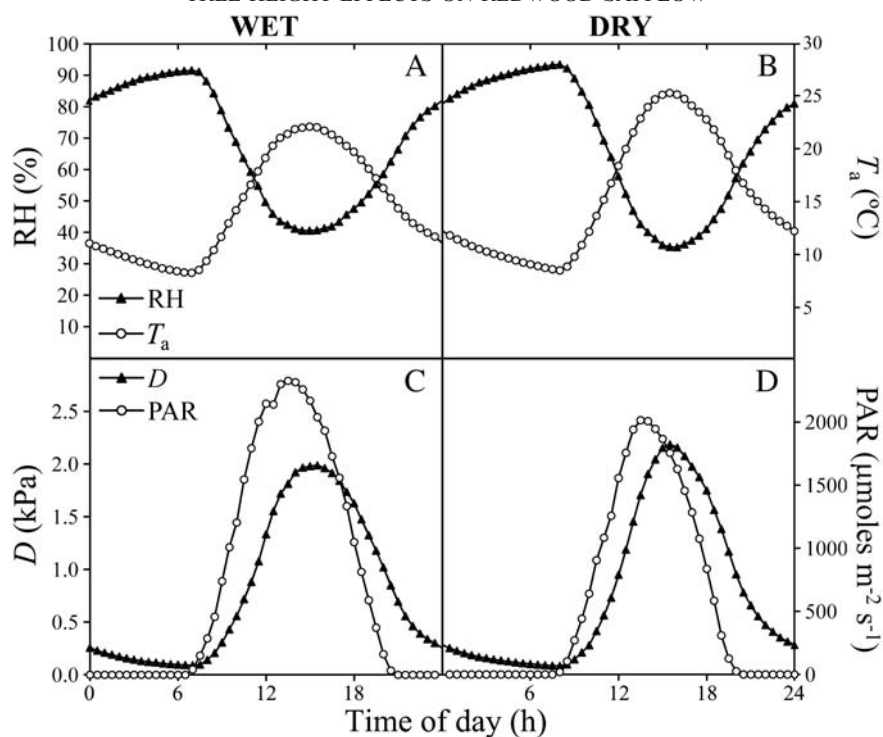
Figure 3. Representative wet (May) and dry (September) season diurnal patterns of (A, B) relative humidity (RH) and air temperature (T_a) and (C, D) vapor pressure deficit (D) and photosynthetically active radiation (PAR) at the study site.

PAR than taller trees. Differences in E_L among height classes were greatest at high D, while differences in G_S among height classes were greatest at low D (Figure 5). Of the 120 separate

regression analyses of G_S' versus $\ln D$, coefficients of determination (R^2) ranged from 0.60 to 0.96 (mean = 0.86), the P-value for 112 of them was <0.0001, and the mean P-value
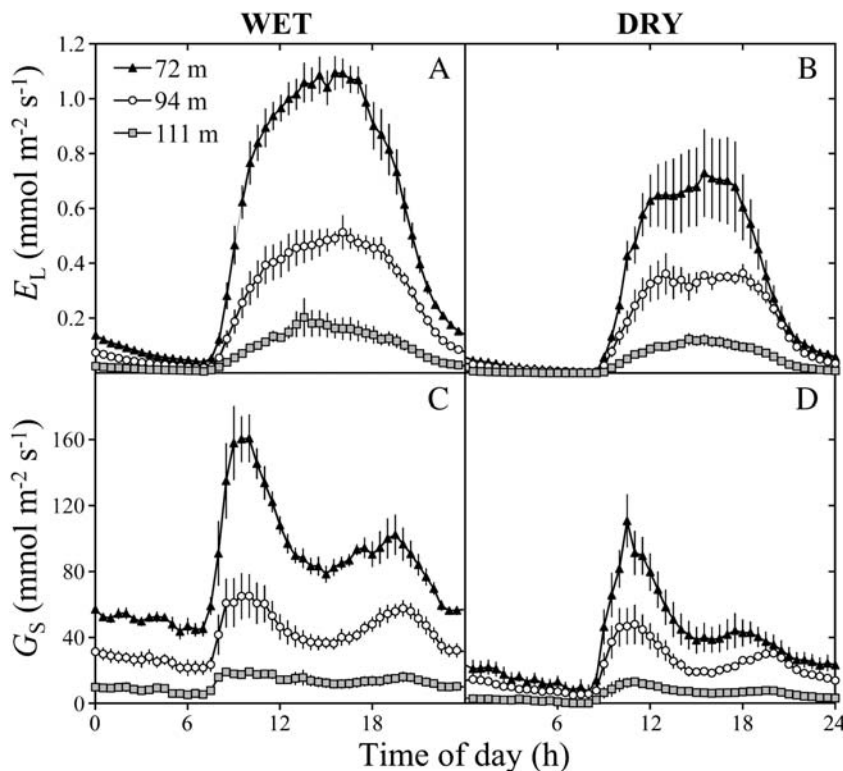

Figure 4. Representative wet (May) and dry (September) season diurnal patterns of (A, B) treetop transpiration (E_L) and (C, D) treetop stomatal conductance (G_S) for three *S. sempervirens* height classes (n = 4 trees/class; mean ± 1 SE).

Table 3. Mean diurnal treetop transpiration (E_L) and treetop average stomatal conductance (G_S) for three *S. sempervirens* height classes ($n = 4$ trees/class) during wet (May) and dry (September) periods in 2008. Values are means for each class with 1 SE of the mean in parentheses. Letters indicate significant differences at $\alpha = 0.05$.

Season	Variable	Height class		
		72 m	94 m	111 m
Wet	E_L (mmol m^{-2} s^{-1})	0.51 (0.03)[a]	0.24 (0.01)[b]	0.08 (0.01)[c]
	G_S (mmol m^{-2} s^{-1})	73.4 (2.2)[a]	34.4 (1.0)[b]	11.0 (0.4)[c]
Dry	E_L (mmol m^{-2} s^{-1})	0.28 (0.02)[a]	0.15 (0.01)[b]	0.04 (0.00)[c]
	G_S (mmol m^{-2} s^{-1})	40.0 (2.2)[a]	22.5 (1.0)[b]	6.4 (0.3)[c]

for the remaining eight was 0.0008. The poorest correlations were for regressions at low and intermediate light levels during the dry season. We focused our analyses on measurements made under high light (PAR > 2000 µmol m^{-2} s^{-1}) and soil moisture conditions in the spring (April–May) to estimate G_{Sref} and $-\delta$ with Eq. (8). Under these conditions, both G_{Sref} and $-\delta$ significantly decreased with increasing tree height ($P < 0.0001$ for both G_{Sref} and $-\delta$, Figures 6 and 7, Table 1). Across all trees, there was a significant, linear relationship between G_{Sref} and $-\delta$ ($P < 0.0001$) with no significant difference between the slope of G_{Sref} and $-\delta$ for *S. sempervirens* (Figure 6) and the hypothesized 0.6 proportionality observed in other species (Oren et al. 1999).

Discussion

Height-related declines in sap flow-derived E_L and G_S in this study are consistent with previous direct measurements of treetop gas exchange capacity in *S. sempervirens* (Ambrose et al. 2009, Mullin et al. 2009). Even though trees in the 94-m height class exhibited similar V_s rates to the 72-m height class, trees in the 94-m height class had lower E_L and G_S rates associated with lower treetop A_S:A_L. Lower E_L and G_S in the 111-m height class, on the other hand, were associated with both lower V_s and lower treetop A_S:A_L compared with trees in either the 72- or 94-m height class. An increase in A_S:A_L with height appears to be a common structural adjustment that can partially compensate for greater resistance to water flow in taller trees (Mencuccini and Grace 1996, Ryan et al. 2000, McDowell et al. 2002a, Delzon et al. 2004). For example, greater A_S:A_L with increasing height in *Fagus sylvatica* resulted in 15% higher G_S in tall trees than would have otherwise occurred (Schäfer et al. 2000). Similarly, greater A_S:A_L and lower minimum Ψ_L with increasing height in *P. menziesii* resulted in 26% higher k_L in tall trees than would have occurred without these adjustments (McDowell
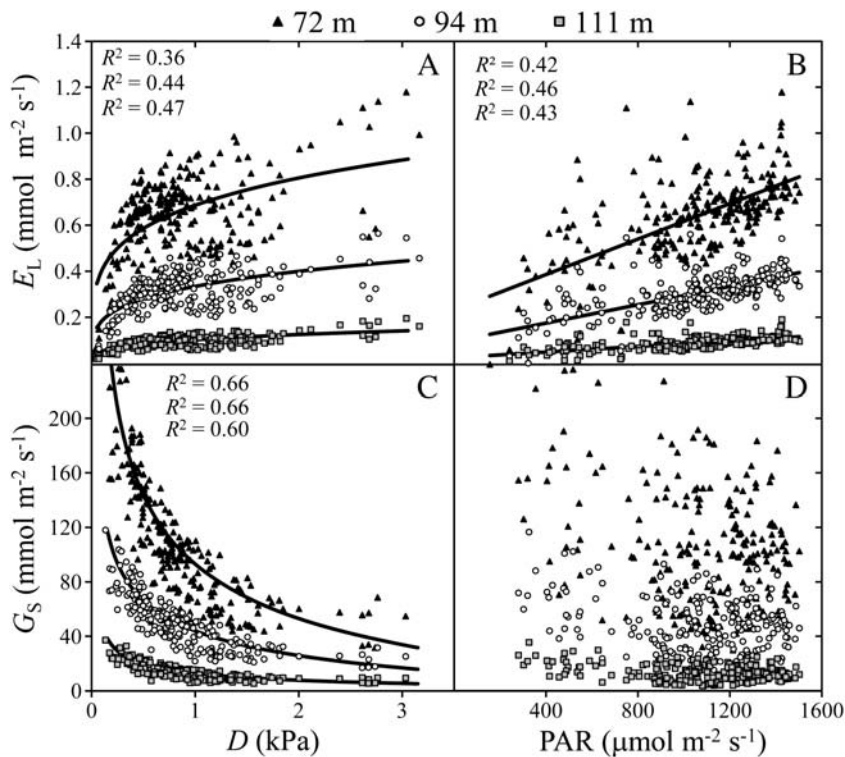

Figure 5. (A–D) Mean daytime total treetop transpiration (E_L) and daytime treetop stomatal conductance (G_S) in three *S. sempervirens* tree height classes ($n = 4$ trees/height class) in relation to mean daily vapor pressure deficit (D) and light (PAR).

Table 4. Equation type and parameters for three height classes used in Figure 5.

Response variable	Environmental variable	Height class (m)	Equation	a	b	c	R^2
E_L	D	72	A	6.8707E−01	2.2911E−01	–	0.36
		94	A	3.3406E−01	2.5704E−01	–	0.44
		111	A	1.0168E−01	2.9211E−01	–	0.47
	PAR	72	B	2.3319E−01	3.8590E−04	–	0.42
		94	B	9.9874E−02	1.9830E−04	–	0.46
		111	B	2.8971E−02	6.1016E−05	–	0.43
G_S	D	72	C	1.8799E+02	−3.4384E−01	−9.4956E+01	0.68
		94	C	9.8114E+01	−2.9472E−01	−5.4091E+01	0.70
		111	C	1.9010E+01	−4.5000E−01	−6.0920E+00	0.70

Parameters a, b and c are from either equation A ($E_L = a * D^b$), B ($E_L = a + b * \text{PAR}$) or C ($G_S = a * D^b + c$), where E_L is daytime average treetop transpiration per unit leaf area, G_S is daytime average treetop stomatal conductance, D is daytime average vapor pressure deficit (kPa) and PAR is daytime average photosynthetic photon flux density (μmol m^{-2} s^{-1}). All relationships are highly significant ($P < 0.0001$).

et al. 2002b). Decreases in A_S:A_L with increasing height that exacerbate rather than alleviate hydraulic limitations can also occur (Phillips et al. 2003; Simonin et al. 2006), but their causes remain unclear (McDowell et al. 2002b). Decreasing A_S:A_L may be accompanied by simultaneous changes in other hydraulic traits, such as an observed increase in K_S that offsets the negative hydraulic effect of decreasing A_S:A_L with increasing height in *Abies balsamea* (Coyea and Margolis 1992). However, in our study trees, A_S:A_L measured at the tree base and base-of-live-crown did not vary significantly with tree height, while A_S:A_L measured at the treetop actually decreased with increasing height (Table 1, Sillett et al. 2010). Therefore, changes in treetop A_S:A_L in our study exacerbated, rather than alleviated, height-related hydraulic constraints, similar to observations made at the whole-tree scale in *Quercus garryana* (Phillips et al. 2003) and *P. ponderosa* (Simonin et al. 2006). These results contrast with previously observed increases in small branch (0.5–1.5 cm diameter) A_S:A_L with increasing height within and among different-sized *S. sempervirens* (Burgess et al. 2006, Ambrose et al. 2009), suggesting

that adjustment of A_S:A_L in *S. sempervirens* may occur at the branch rather than trunk level. Conifer branches typically have much higher hydraulic resistances and steeper axial tension gradients than trunks (Zimmermann 1983, Tyree and Ewers 1991, Domec and Gartner 2003, Domec et al. 2006, 2008). Increases in small branch rather than trunk A_S:A_L with height in *S. sempervirens* treetops presumably occur to compensate for hydraulic constraints where it would be most beneficial and may be a mechanism that maximizes total treetop light interception and carbon uptake capacity even though stomatal
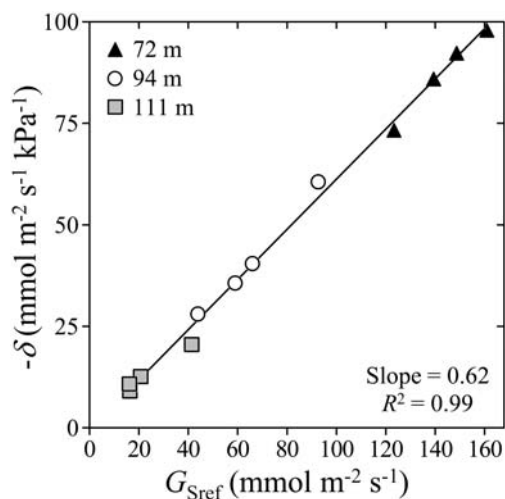

Figure 6. Relationship between average treetop stomatal conductance at a reference vapor pressure deficit (G_{Sref}; $D = 1$ kPa) and sensitivity of average treetop stomatal conductance to vapor pressure deficit ($-\delta$; $dG_S/d\ln D$) calculated for each study tree using data after applying filters and boundary line analysis as described in the text (G_S') and Eq. (8).
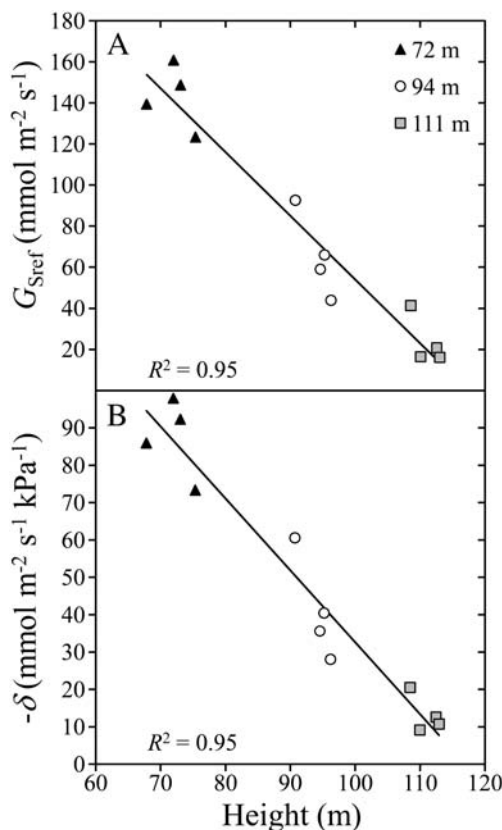

Figure 7. (A) Decline in average treetop stomatal conductance at a reference vapor pressure deficit (G_{Sref}; $D = 1$ kPa) with increasing *S. sempervirens* tree height. (B) Decline in sensitivity of average treetop stomatal conductance to vapor pressure deficit ($-\delta$; $dG_S/d\ln D$) with increasing *S. sempervirens* tree height.

conductance declines on a per unit leaf area basis (Buckley and Roberts 2005).

Our results support the hypothesis that environmental sensitivity of treetop gas exchange in *S. sempervirens* is strongly influenced by height. Changes in E_L and G_S were lower in taller trees on both diurnal and seasonal time scales and in response to changing PAR and D. Differences in E_L and G_S among different-sized trees were also greater during the spring than during the late summer when soil and atmospheric moisture were more limiting. These results are similar to those observed in *P. menziesii* (McDowell et al. 2005) and provide further evidence that size-related hydraulic limitations to gas exchange are greater during relatively wet and mild conditions than during hot and dry conditions. The large differences in treetop G_S among height classes during the period of maximum leaf development in the spring agree with treetop leaf $\delta^{13}C$ data indicating greater stomatal limitation of gas exchange with increasing height in *S. sempervirens* (Ambrose et al. 2009). Although an increase in leaf $\delta^{13}C$ could also have occurred through an increase in photosynthetic capacity due to light acclimation, treetop light availability did not significantly differ among height classes, and direct gas exchange measurements show decreasing photosynthesis with increasing height in *S. sempervirens* (Ambrose et al. 2009, Mullin et al. 2009), suggesting that differences in photosynthetic capacity were not the primary cause of observed height trends in $\delta^{13}C$.

The tops of shorter *S. sempervirens* trees showed higher G_{Sref} as well as higher sensitivity to changes in D ($-\delta$) and a greater absolute reduction in G_S with increasing D than taller trees. The positive correlation between G_{Sref} and $-\delta$ in our study is consistent with previous observations across many species, environmental conditions and tree sizes (e.g., Oren et al. 1999, 2001, Schäfer et al. 2000, Ewers et al. 2001, 2005, Addington et al. 2004, 2006, Delzon et al. 2004). In addition, the slope of the relationship between G_{Sref} and $-\delta$ in *S. sempervirens* is not significantly different from the theoretical proportionality (0.6) that results from stomatal regulation of E_L and Ψ_L (Oren et al. 1999). Short trees with high G_S require higher sensitivity to D to avoid excessive water losses and maintain favorable Ψ_L. If tall trees with low G_S had the same sensitivity as short trees with high G_S, rates of gas exchange in tall trees would reach zero very quickly. Lowered G_S sensitivity to D in taller trees ensures a more stable carbon uptake rate over a wide range in daily and seasonal D (Schäfer et al. 2000). These differences in sensitivity explain why E_L and G_S rates observed at the tops of taller *S. sempervirens* trees were low but also more stable than the tops of shorter trees over the course of the day as well as over the growing season.

Our measurements were only made at treetops, and it is unknown whether observed differences in stomatal sensitivity among height classes apply to entire crowns. Nevertheless, these results suggest that shorter *S. sempervirens* trees may be able to take better advantage of optimal growing conditions when soil and atmospheric water are abundant but will also have greater absolute declines in gas exchange rates than taller trees when conditions become less favorable. Differences in environmental sensitivity among trees of different heights imply that they will exhibit different responses to changing climate. The height-related trends in G_S sensitivity that we observed are an inevitable consequence of maximum G_S being lower in the taller trees, and reduced sensitivity of G_S to D does not necessarily imply that the stomata themselves are inherently less sensitive to D. Detailed examination of stomatal density and anatomy as well as more direct leaf gas exchange measurements are needed to determine whether inherent stomatal sensitivity varies with *S. sempervirens* tree height. There is evidence that osmotic adjustment, or active accumulation of symplastic solutes as a mechanism for maintaining cell turgor and volume with increasing height, is closely related to G_S sensitivity to D and may function to maintain G_S under conditions of greater evaporative demand (Woodruff et al. 2010). Additional examination of the potential carbon cost of osmotic adjustment and its role in influencing the relationship between G_S and D in different-sized *S. sempervirens* is warranted.

Our study demonstrates that treetop E_L and G_S in *S. sempervirens* decrease with increasing height regardless of any compensating adjustments that may be present and represents the first effort to document these patterns in trees approaching their maximum known height. Higher water flux rates at the tops of short *S. sempervirens* trees are also associated with higher sensitivity to soil and atmospheric moisture, consistent with the role of stomata in regulating minimum Ψ_L and preventing excessive xylem cavitation. Despite their lower stomatal sensitivity to D, the tops of taller *S. sempervirens* trees will likely reach minimum Ψ_L earlier in the day and remain there for a longer period of time than shorter trees, leading to lower daily integrated G_S and photosynthesis (Yoder et al. 1994). In addition to lower G_S, increasing hydrostatic effects on leaf morphology and anatomy with increasing height also limit net carbon gain in *S. sempervirens* through reduced internal CO_2 conductance and higher dark respiration rates (Ambrose et al. 2009, Mullin et al. 2009, Oldham et al. 2010). Repeated direct measurements show a negative correlation between height growth and total height in our study trees (Sillett et al. 2010). We do not currently know whether lower photosynthesis in taller *S. sempervirens* directly translates into lower rates of treetop carbon uptake and height growth, or whether the decrease in treetop $A_S:A_L$ in taller trees completely offsets reduced assimilation at the leaf scale. Furthermore, it is unclear whether height growth in tall trees is actually limited by carbon supply (Ryan et al. 2006). In 6- to 35-m tall *P. ponderosa*, for example, it appears that height growth is not limited by carbon supply but rather sink limitations (Sala and Hoch 2009). Observed seasonal reductions in carbohydrate pools suggest that carbon limitations may adversely affect height growth in tall *S. sempervirens* (Bentrup 2009). In addition, aging effects via increasing stem respiration may contribute to slower height growth in our study trees (Sillett et al. 2010). We are currently lacking information on carbon sinks, storage and allocation patterns both above- and below-ground necessary to determine whether height growth in *S. sempervirens* is actually carbon

limited. We focused our measurements on treetop water flux dynamics in order to isolate hydraulic limitations in the location of most relevance to height growth. Additional measurements that explicitly link hydraulic architecture, water transport, carbon balance and growth at the whole-tree scale are necessary in order to better understand hydraulic limitations, compensations and consequences in *S. sempervirens* and other tall trees.

Funding

Acknowledgments

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