

Hydrostatic constraints on morphological exploitation of light in tall *Sequoia sempervirens* trees

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Abstract We studied changes in morphological and physiological characteristics of leaves and shoots along a height gradient in *Sequoia sempervirens*, the tallest tree species on Earth, to investigate whether morphological and physiological acclimation to the vertical light gradient was constrained by hydrostatic limitation in the upper crown. Bulk leaf water potential (Ψ) decreased linearly and light availability increased exponentially with increasing height in the crown. During the wet season, Ψ was lower in the outer than inner crown. C isotope composition of leaves ($\delta^{13}\text{C}$) increased with increasing height indicating greater photosynthetic water use efficiency in the upper crown. Leaf and shoot morphology changed continuously with height. In contrast, their relationships with light availability were discontinuous: morphological characteristics did not correspond to increasing light availability above 55–85 m. Mass-based chlorophyll concentration (chl) decreased with

increasing height and increasing light availability. In contrast, area-based chl remained constant or increased with increasing height. Mass-based maximum rate of net photosynthesis (P_{max}) decreased with increasing height, whereas area-based P_{max} reached maximum at 78.4 m and decreased with increasing height thereafter. Mass-based P_{max} increased with increasing shoot mass per area (SMA), whereas area-based P_{max} was not correlated with SMA in the upper crown. Our results suggest that hydrostatic limitation of morphological development constrains exploitation of light in the upper crown and contributes to reduced photosynthetic rates and, ultimately, reduced height growth at the tops of tall *S. sempervirens* trees.

Keywords Hydrostatic limitation · Light interception · Maximum tree height · Morphological plasticity · Water use efficiency

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Introduction

As trees grow taller, increasing path length through which water must travel to reach transpiring leaves and increasing gravitational potential ($0.0098 \text{ MPa m}^{-1}$, Zimmermann 1983) lead to increasing water stress at the treetop. The hydraulic limitation hypothesis (Ryan and Yoder 1997) proposes that this reduces stomatal conductance and integrated photosynthesis, ultimately limiting height growth. This hypothesis has stimulated much research on changes in physiological properties of trees with increasing age and size (Ryan et al. 2006). However, the critical link between physiological changes and growth reduction is not yet completely understood. For example, reduced stomatal conductance alone is not sufficient to explain photosynthesis decline in tall trees (Niinemets 2002; Martínez-

Vilalta et al. 2007). Although the decline in photosynthesis accounts for the decline in wood growth (Ryan et al. 2004), hydraulic limitation is not always responsible for decreased canopy photosynthesis (Barnard and Ryan 2003). Theoretical and empirical studies suggest that there may be homeostatic mechanisms that compensate, at least in part, for reduced hydraulic conductance as trees grow taller (Becker et al. 2000; Magnani et al. 2000; Mencuccini and Magnani 2000; Ryan et al. 2006; Burgess et al. 2006). Mechanisms underlying the reduction in height growth with increasing tree height may be more complex than proposed by the original hydraulic limitation hypothesis (Mencuccini and Magnani 2000; Niinemets 2002; Buckley and Roberts 2005; Martínez-Vilalta et al. 2007).

In addition to changes in hydraulic properties, morphological and biochemical properties of foliage also change with increasing height. Vertical changes in leaf and shoot morphology from lower- to upper-crown positions have been attributed mostly to increasing light availability (Niinemets and Kull 1995a, b; Sprugel et al. 1996; Stenberg et al. 2001; Cescatti and Zorer 2003). This is reflected in textbook terms such as “sun” versus “shade” leaf/shoot (Kozłowski and Pallardy 1996). In conifers, leaves on well-illuminated shoots tend to be thick, small, and three-dimensionally arranged along the shoot axis, whereas leaves on shaded shoots are flat, large, and planarly arranged along the shoot axis to maximize efficiency of light interception (Leverenz 1996). In tall trees, however, light availability may not be the only factor influencing the vertical variation in leaf and shoot morphology (Koch et al. 2004). For example, in 60-m-tall *Pseudotsuga menziesii* (Mirb.) Franco. var. *menziesii* trees, cell expansion and cell division are negatively affected by decline in turgor pressure caused by the hydrostatic gradient, resulting in shorter leaves and shoots in the upper crown (hydrostatic limitation, Woodruff et al. 2004). In the upper crown of tall trees, hydrostatic limitation may constrain various physiological processes and contribute to reduced height growth. Under constant water stress, leaf water potential may be adjusted osmotically through greater C allocation to non-structural, soluble carbohydrates (Morgan 1984; Niinemets and Kull 1998) rather than to growth. Morphological and biochemical properties that increase tolerance to water stress, such as greater leaf mass per unit area (LMA) and higher lignin content may decrease the rate of CO₂ diffusion within leaves (Parkhurst 1994; Niinemets and Kull 1998; Hanba et al. 1999), resulting in decreased photosynthetic rate. Greater LMA may also increase respiration rate per leaf surface area, resulting in reduced net C gain (Koch et al. 2004). Although the hydraulic limitation hypothesis did not emphasize any role of morphological changes (Ryan et al. 2006), morphological and biochemical constraints on C gain may be additional factors contributing to reduced

height growth in tall trees (Köstner et al. 2002; Niinemets 2005).

In *Sequoia sempervirens* (D. Don.) Endl. (coast redwood), the tallest living tree species, increasing respiratory demand caused by changes in leaf and shoot morphology, combined with decreasing xylem pressure potential and photosynthetic capacity, may limit growth rates at the treetop and contribute to a theoretical maximum height (Koch et al. 2004). In this species, marked changes in leaf and shoot morphology occur along the vertical gradient (Koch et al. 2004, their Fig. 2). Lower-crown leaves of *S. sempervirens*, particularly those of saplings and basal sprouts, resemble shade leaves of true firs (*Abies* spp.) or yews (*Taxus* spp.). Leaves are long, flat, and planarly arranged along the shoot axis in the lower crown, becoming shorter, thicker, and more closely appressed to the shoot axis with increasing height such that leaves in the upper crown more closely resemble those of juniper (*Juniperus* spp.). This great morphological plasticity may contribute to one of the distinguishing ecological features of old-growth *S. sempervirens* forests: from saplings to mature trees, foliage exists at all heights within canopies over 100 m deep, resulting in the highest leaf area index observed for forest ecosystems (Westman and Whittaker 1975; Fujimori 1977; Sillett and Van Pelt 2007). The causal factors underlying morphological variation in *S. sempervirens* foliage, however, are poorly understood.

In this study, we investigated changes in morphological and physiological characteristics of leaves and shoots in relation to the vertical gradient in several of the tallest *S. sempervirens* trees known, ranging from 97 to over 112 m in height. We postulated that light environment is the primary factor determining shoot and leaf morphology in the lower crown. With increasing height, hydrostatic limitation may constrain morphological development and reduce correlations between the light environment and shoot/leaf morphology in the upper crown. Constraints on morphological development may induce reductions in photosynthetic capacity and, ultimately, height growth. Whereas previous studies comparing trees of different sizes included confounding effects of ontogeny and site conditions (e.g., Yoder et al. 1994; Phillips et al. 2002; Thomas and Winner 2002; McDowell et al. 2005), studies on tall *S. sempervirens* trees offer a unique opportunity to observe vertical gradients within crowns of single trees over 80 m deep.

Materials and methods

Study site

Our study was conducted in old-growth *S. sempervirens* forests at Prairie Creek Redwoods State Park (PCRSP) and

Humboldt Redwoods State Park (HRSP), California, USA. Study trees (Table 1) were all located on alluvial flats within intact stands. Trees were not selected randomly but were chosen for height and accessibility. Mean elevation and annual precipitation at the two sites are 90 m and 1,718 mm, respectively (PCRSP, precipitation from Orick, California) and 100 m and 1,233 mm, respectively (HRSP, precipitation from Scotia, California). Both sites experience a coastal-Mediterranean climate with most precipitation occurring during winter and substantial fog occurring during the summer.

Leaf water potential and C isotope composition

From autumn of 2000 to winter of 2001, we accessed the crowns of ten *S. sempervirens* trees (Table 1) using single-rope and arborist-style techniques (Moffett and Lowman 1995; Jepson 2000). In each tree, we sampled 30- to 50-cm-long foliated branch tips from small inner-crown branches 1–3 m away from the main trunk at 10-m height intervals from the tree top. We also sampled from outer-crown locations near the ends of branches up to 14 m away from the main trunk. The inner-crown samples were intended to observe the effects of height while excluding effects of branch length on hydraulic properties. The outer-crown samples were intended to increase the range of light environments sampled. For each tree, we collected at least one pair of inner- and outer-crown samples from the same height.

Table 1 Structural attributes of the *Sequoia sempervirens* trees studied in northern California [Prairie Creek Redwoods State Park (P) and Humboldt Redwoods State Park (H)]. Values are for 2001. Heights of several trees have increased (e.g., Stratosphere was 113.0 m and Paradox was 112.5 m in 2007). DBH diameter at breast height

Tree name	Tree height (m)	DBH (cm)
Stratosphere ^{a,c} (H)	112.3	521
Federation ^a (H)	112.2	440
Paradox ^a (H)	111.9	379
Pipe dream ^{a,c} (H)	111.2	495
Millenium ^{a,c} (H)	111.1	277
Dometop ^c (H)	109.1	393
Adventure ^{a,b} (P)	101.3	464
Zeus ^{a,b,c} (P)	101.0	519
Poseidon ^{a,b,c} (P)	99.1	439
Demeter ^a (P)	97.5	434
Ballantine ^a (P)	97.2	518
Yin ^a (P)	97.0	375

^a Trees used for water potential and $\delta^{13}\text{C}$ measurement (2000–2001)

^b Trees used for detailed morphology measurement (2005)

^c Trees used for photosynthesis measurement (2003 and 2005)

We measured predawn and midday bulk leaf water potentials (Ψ) at the base of second-year growth increments using a Scholander–Hammel pressure chamber (model 600; PMS Instruments, Corvallis, Ore.). Measurements were made during the dry and wet seasons (October 2000 and January 2001, respectively). Measurements of three sample shoots were averaged to obtain the mean value at each location.

To quantify the light environment of each sample, we took hemispherical photographs on overcast days using a digital camera on a self-leveling mount. The hemispherical photographs were analyzed using WinScanopy (version 2002a; Régent Instruments) to calculate canopy openness, total radiation simulated for the 12-month growing season, direct site factor (proportion of direct radiation received), indirect site factor (proportion of diffuse radiation received), and total site factor (proportion of total radiation received).

We sampled three second-year shoot increments at each location for measurement of morphology and water-use efficiency. We measured projected area of the sample shoots (A_S) using a digital area meter (DIAS; Delta T Devices, Cambridge, MA). The shoots were then oven-dried at 70°C to constant weight to determine dry mass. We calculated shoot mass per unit area (SMA; g m^{-2}) as the ratio of shoot dry mass (M_S) to A_S . SMA is a measure of light interception efficiency (i.e., dry matter investment relative to light-capturing area) of shoots (Niinemets and Kull 1995b).

C isotope composition ($\delta^{13}\text{C}$) of second-year foliage was analyzed at the Colorado Plateau Stable Isotope Laboratory, Flagstaff, Arizona (<http://www4.nau.edu/cpsil/>). The leaf samples were oven-dried at 70°C and ground to 40 mesh. Then, a subsample was pulverized, encapsulated in tin, and combusted at 1,000°C (NC2100; Elantech, Lakewood, N.J.). The resultant CO_2 was purified and its $^{13}\text{CO}_2/^{12}\text{CO}_2$ ratio was analyzed by isotope-ratio mass spectrometry (Delta Plus XL; ThermoQuest Finnigan, Bremen) in continuous-flow mode. $\delta^{13}\text{C}$ (‰) values were expressed as the relative abundance of ^{13}C versus ^{12}C compared with a standard (Pee Dee Belemnite):

$$\delta^{13}\text{C} = \left\{ \left(R_{\text{sam}} / R_{\text{std}} \right) - 1 \right\} \times 1000, \quad (1)$$

where R_{sam} and R_{std} are the $^{13}\text{C}/^{12}\text{C}$ ratios of the sample and standard, respectively. The SD of repeated measurements of secondary standard material was 0.1‰ (external precision). $\delta^{13}\text{C}$ reflects the ratio of substomatal to ambient CO_2 concentration (C_i/C_a). Less negative values of $\delta^{13}\text{C}$ indicate lower C_i/C_a and greater time-integrated photosynthetic water-use efficiency (C gain per water transpired) of leaves under field conditions (Farquhar et al. 1989).

Morphology and photosynthesis

In autumn 2005, we climbed and intensively sampled three *S. sempervirens* trees (Table 1) using similar techniques and procedures as in 2000. For each tree, we sampled from both inner- and outer-crown branches at each height (15-m intervals from the treetop). Hemispherical photographs taken at each location were analyzed using Gap Light Analyzer version 2 (Frazer et al. 2001) to calculate canopy openness, total radiation simulated for the 12-month growing season, direct site factor, indirect site factor, and total site factor. Comparison of these measures of light availability derived by Gap Light Analyzer showed close agreement with those derived from WinScanopy using the same photographs (slope = 0.91–0.96, $R^2 = 0.96$ –0.98).

For quantification of shoot morphology, we sampled five second-year shoot increments from each location. The length of each sample shoot (L_S) was measured to the nearest 0.1 mm. We photographed each sample shoot from the adaxial side (0° shoot inclination and rotation angles, Stenberg et al. 1998) in front of a slide viewer using a digital camera (Niinemets 2005). This uniformly illuminated the background and created a silhouette image of the shoot. We then detached all leaves from the twig, placed them on the slide viewer and flattened them with a 1-cm-thick Plexiglas sheet and photographed them to obtain the projected image. We analyzed shoot and leaf photographs using an image analysis program (Image-J; National Institute of Health, USA) to obtain shoot silhouette area (A_S) and projected leaf area (A_L). All leaves and twigs were oven-dried to constant weight at 70°C to determine shoot dry mass (M_S , including both leaves and twig) and leaf dry mass (M_L).

To determine foliar chlorophyll (chl) content we sampled five additional second-year shoot increments from each location. All leaves were detached from the twig, mixed thoroughly, and 0.3–0.5 g fresh mass of the leaves was subsampled for chl analysis. The remaining leaves were weighed to obtain the fresh mass and oven-dried at 70°C to constant weight to determine dry mass. The dried samples were used to calculate the fresh mass to dry mass ratio of leaves. Leaves for chl analysis were ground in 80% (v/v) acetone for chl extraction. Chl absorption of the extract was measured using a double-beam spectrophotometer (UVIDEC-340; Japan Spectroscopic, Tokyo). The volumetric concentrations of chl *a* and chl *b* (mg l^{-1}) of the extract were determined following methods described in Porra et al. (1989). The volumetric chl concentration was converted to chl content per leaf dry mass (mg g^{-1}) using the fresh weight to dry mass ratio of the dried samples.

We measured photosynthetic capacity using cut branches obtained from six trees in 2003 and 2005 (Table 1). We cut 50-cm-long branches from the trees with pruning

shears, submerged the cut end in water while still in the tree, and then re-cut to remove 20 cm of stem length. The cut end of the branch was sealed in a plastic test tube filled with water, transported to the laboratory, and allowed to rehydrate for a minimum of 6 h, at which time water potentials of twigs were -0.5 MPa or higher. We measured light-saturated maximum rate of net photosynthesis (P_{max}) of second-year foliage using the LI-6400 portable gas exchange system fitted with a 6400-02B LED light source (Li-Cor, Lincoln, Neb.). Air temperature, vapor pressure deficit, and CO_2 concentration in the cuvette were maintained at $22.5 \pm 0.8^\circ\text{C}$, 1.3 ± 0.2 kPa, and 366 ± 4 $\mu\text{mol mol}^{-1}$, respectively (mean \pm SD). Light-saturated maximum rate of net photosynthesis (P_{max}) was measured at $2,000$ $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density. Foliage within the leaf chamber was cut at the chamber boundary, and A_S , M_S , and SMA were measured using the same methods as in 2000. A_S and M_S were used to calculate area- and mass-based P_{max} . The photosynthetic rates presented here for leaves on detached, rehydrated shoots were similar to those measured in situ in high light. For 37 measurements in three trees at heights from 95 to 105 m, area- and mass-based P_{max} averaged 8.20 ± 7.28 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 4.80 ± 1.75 $\text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$, respectively (mean \pm SD, data not shown).

Statistical analyses

We used regression analysis to examine changes in Ψ and light availability in relation to height as well as changes in SMA and $\delta^{13}\text{C}$ in relation to height and light availability. We used ordinary least-squares regression to investigate changes relative to height. First, tree and crown position (inner or outer crown) were included as independent variables in the regression. There was significant variation among trees for all variables, but the variability could not be interpreted within the scope of our data (e.g., tree size, location, site condition). Therefore, we chose to pool the data to look for universal trends with height.

We observed a discontinuous transition point in the variation in SMA and $\delta^{13}\text{C}$ in relation to light availability (I), such that both variables were highly correlated with light in the lower crown, but the relationships became weaker in the upper crown. This indicated that linear approaches such as multiple regression could not be used to distinguish the effects of height versus light on these variables. Therefore, we fit a combination of two linear regressions (piecewise regression) to estimate the height above which the effect of light became weak or was lost, as follows:

$$\begin{cases} y = a_1 + b_1 I & [I < q] \\ y = a_2 + b_2 I & [q \leq I] \end{cases} \quad (2)$$

where y is the dependent variable (SMA or $\delta^{13}\text{C}$). The transition point of the relationship (q) was estimated iteratively using the non-linear regression function in Systat version 9.0 (SPSS, Chicago, IL). Parameters a_1 , b_1 , a_2 and b_2 were estimated by reduced major axis regression to account for variation in both the dependent and independent variables, as well as for large differences in data range between the independent and dependent variables (Sokal and Rohlf 1995; McArdle 1988).

From the detailed analysis of leaf and shoot morphology, we calculated the following indices to characterize light interception efficiency:

$$\text{LMA} = M_L/A_L \quad (3)$$

$$\text{SMA} = M_S/A_S \quad (4)$$

$$\text{SPAR} = A_S/A_L \quad (5)$$

LMA (g m^{-2}) and SMA (g m^{-2}) represent dry matter investment relative to light-capturing area of leaves and shoots, respectively (Niinemets and Kull 1995a, b). The shoot silhouette area to projected leaf area ratio (SPAR) is a measure of leaf overlap within the shoot and reflects the efficiency of leaf display (Oker-Blom and Smolander 1988). We analyzed leaf and shoot morphology and chl content in relation to height and light availability using the same methods as described above. Finally, we analyzed changes in mass- and area-based P_{max} in relation to height and SMA using ordinary least-squares regression and reduced major axis regression, respectively.

Results

Leaf water potential and C isotope composition

Ψ decreased linearly with increasing height (Table 2; Fig. 1a, b). During the wet season, the vertical gradients in both predawn and midday Ψ conformed to the hydrostatic gradient. During the dry season, vertical gradients in both predawn and midday Ψ were slightly steeper than the hydrostatic gradient. During the wet season, Ψ was lower in the outer than inner crown ($F = 9.05$, $P = 0.003$ and $F = 17.57$, $P < 0.001$ for predawn and midday, respectively). In contrast, dry season Ψ was not affected by crown position ($F = 1.66$, $P = 0.199$ and $F = 1.62$, $P = 0.206$ for predawn and midday, respectively).

Light availability increased exponentially with increasing height (Table 2). Of the various measures of light availability, canopy openness (I_{CO}) had the highest correlation with height (Fig. 1c), and is used to represent light availability hereafter. Although I_{CO} was higher than the regression estimate for some outer canopy positions (e.g., 75 m in Ballantine and 100 m in Paradox), there was no

Table 2 Parameter estimates ($\pm 95\%$ confidence interval) for regression equations describing the vertical change in leaf water potential (Ψ) and light availability (I) in relation to height (H , m) for the ten tall *S. sempervirens* trees studied in northern California. Linear and exponential equations of the form: $\Psi = \alpha_0 + \beta_0 H$ and $I = \alpha_1 \exp(\beta_1 H)$ were fitted to the pooled data for all ten trees

Response variable		Parameters		R^2
		α_0	β_0	
Ψ (MPa)	Wet season Predawn	-0.09 ± 0.07	-0.0107 ± 0.0009^a	0.725
	Wet season Midday	-0.33 ± 0.13	-0.0100 ± 0.0016^a	0.421
	Dry season Predawn	-0.16 ± 0.03	-0.0108 ± 0.0004	0.910
	Dry season Midday	-0.58 ± 0.06	-0.0113 ± 0.0008	0.762
Light availability		α_1	β_1	R^2
Canopy openness (%)		1.98 ± 1.33	0.028 ± 0.007	0.520
Direct site factor		0.02 ± 0.02	0.029 ± 0.011	0.353
Indirect site factor		0.03 ± 0.02	0.027 ± 0.008	0.381
Total site factor		0.02 ± 0.02	0.028 ± 0.010	0.364

^a 95% confidence interval includes $-0.0098 \text{ MPa m}^{-1}$

significant effect of crown position on light availability overall ($F = 2.24$, $P = 0.141$).

SMA and C isotope composition ($\delta^{13}\text{C}$) both increased linearly with increasing height (Fig. 2a, b). Both SMA and $\delta^{13}\text{C}$ were higher in the outer than inner crown ($F = 6.28$, $P = 0.016$ and $F = 5.29$, $P = 0.026$, respectively). In contrast to the linear trend with height, both variables increased discontinuously with increasing I_{CO} (Fig. 2c, d). SMA increased markedly with increasing I_{CO} in the lower crown but was not correlated with I_{CO} in the upper crown. The transition point of the relationship was 25.5%. I_{CO} greater than 25.5% was not observed in the study trees below 85 m. Similarly, $\delta^{13}\text{C}$ varied widely in the lower crown, ranging from -31.4 to -25.7‰ between 7.0 and 16.9% I_{CO} . In the upper crown, $\delta^{13}\text{C}$ was not correlated with I_{CO} . The transition point of the relationship was 18.1%. I_{CO} greater than 18.1% was not observed in the study trees below 75 m.

Morphology and photosynthesis

All measures of shoot size decreased continuously with increasing height (Fig. 3a–e). M_L and M_S both decreased exponentially with increasing height (Fig. 3a, b). The rates of decrease were relatively small: 1.5 and 1.4% per meter for M_L and M_S , respectively. L_S decreased linearly with increasing height at the rate of -0.44 mm/m (Fig. 3c). A_L and A_S both decreased exponentially with increasing height at rates greater than those of mass: 2.6 and 3.7% per meter, respectively (Fig. 3d, e). Because leaf and shoot area decreased more rapidly with height than mass, both LMA and SMA increased exponentially with height at an average

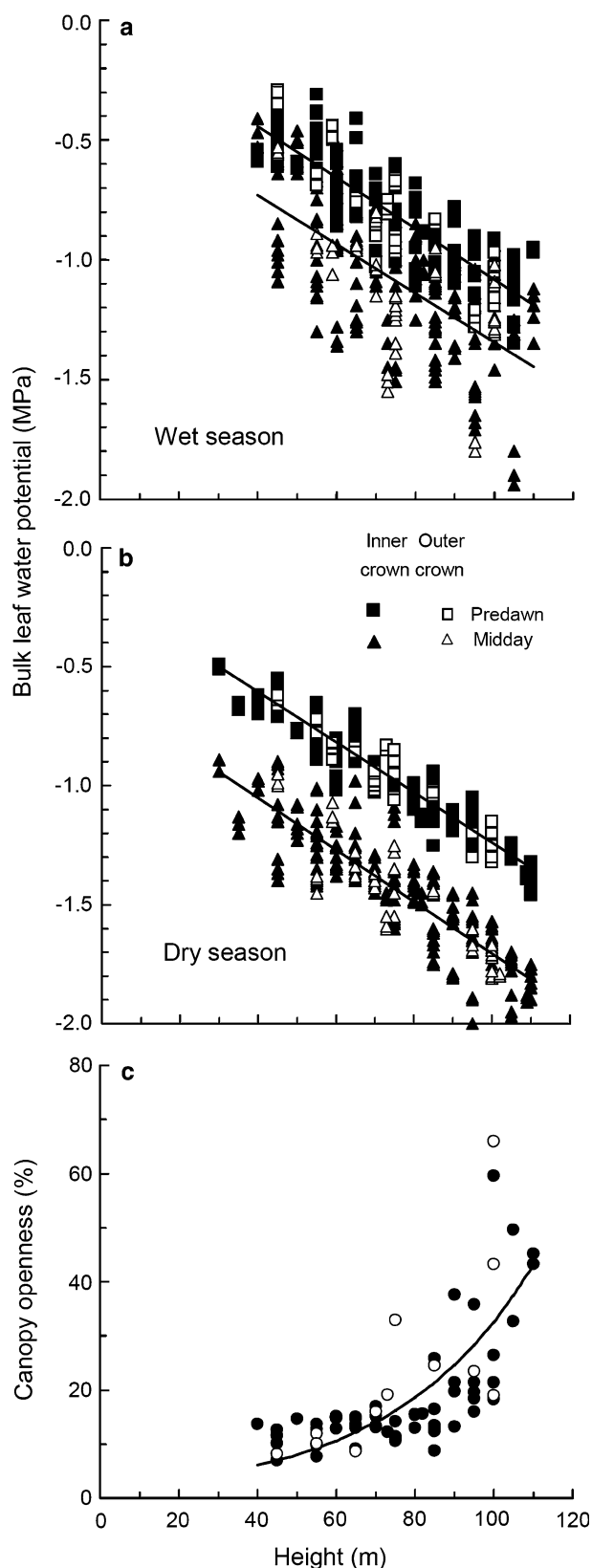


Fig. 1a–c Predawn and midday bulk leaf water potential during the wet and dry seasons and canopy openness (I_{CO}) in relation to height for ten tall *Sequoia sempervirens* trees

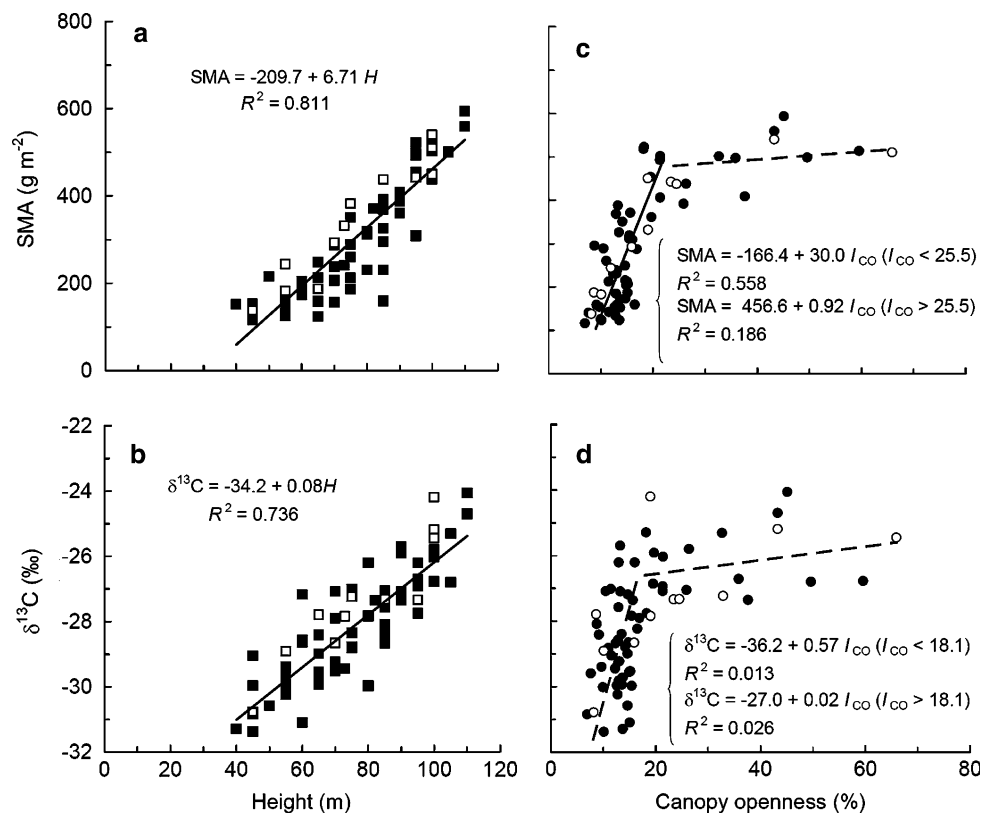
rate of 1.1 and 2.3% per meter, respectively (Fig. 3f, g). SPAR (A_S/A_L) decreased linearly with increasing height (Fig. 3h). For shoots at the bottom of the crown, SPAR was nearly 1, indicating very little overlap among leaves within the shoot. However at 100 m, SPAR decreased to 0.4, indicating considerable leaf overlap within the shoot with less than half of the leaf area exposed to light. Only LMA and SMA were affected by crown position, such that both were higher in the outer than inner crown ($F = 5.66$, $P = 0.026$ and $F = 4.92$, $P = 0.036$ for LMA and SMA, respectively).

All measures of shoot size decreased discontinuously with I_{CO} (Fig. 4a–e). M_L and M_S both decreased markedly with increasing I_{CO} in the lower crown, but the relationships were not significant (Fig. 4a, b; Table 3). Above 12.6%, neither M_L and M_S was correlated with I_{CO} . I_{CO} greater than 12.6% was not observed in the study trees below 55 m. Shoot length decreased linearly with increasing I_{CO} to 29.0%, above which there was no correlation with I_{CO} (Fig. 4c). I_{CO} greater than 29.0% was not observed in the study trees below 85 m. A_L and A_S both decreased markedly with increasing I_{CO} in the lower crown (Fig. 4d, e). However, both A_L and A_S changed very little with I_{CO} above 12.6%. Both LMA and SMA increased markedly with increasing I_{CO} in the lower crown (Fig. 4f, g). However, the slopes decreased markedly in the upper crown above 15.2 and 20.0% for LMA and SMA, respectively. SPAR decreased markedly with increasing I_{CO} in the lower crown (Fig. 4h). However, SPAR was not correlated with I_{CO} above 16.3%. I_{CO} greater than 16.3% was not observed in the study trees below 70 m.

Mass-based chl concentration (i.e., chl content per leaf mass) decreased linearly with increasing height at an average rate of $-0.047 \text{ mg g}^{-1}/\text{m}$ (Fig. 5a). In contrast, chl content per leaf area did not vary with height (Fig. 5b) and chl content per shoot area increased linearly with increasing height at an average rate of $0.008 \text{ g m}^{-2}/\text{m}$ (Fig. 5c). Mass-based chl concentration was lower in the outer than inner crown ($F = 5.68$, $P = 0.025$), whereas area-based chl concentrations were not affected by crown position ($F = 0.001$, $P = 0.974$ and $F = 1.36$, $P = 0.255$ for A_L and A_S , respectively).

Mass-based chl concentration decreased continuously with increasing I_{CO} (Fig. 5d), and there was no clear transition point in the relationship (Table 3). However, the rate of change decreased with increasing I_{CO} such that, above 27.5%, mass-based chl concentration was not correlated with I_{CO} ($R^2 = 0.283$, $P = 0.113$). Chl content per leaf area decreased linearly with increasing I_{CO} (Fig. 5e, $R^2 = 0.174$, $P = 0.017$). In contrast, chl content per shoot area increased markedly with increasing I_{CO} in the lower crown but was not correlated with I_{CO} in the upper crown above 25.9% (Fig. 5f; Table 3).

Fig. 2a–d Shoot mass per area (SMA) and leaf C isotope composition ($\delta^{13}\text{C}$) in relation to height and I_{CO} for ten tall *S. sempervirens* trees. Open symbols denote outer-crown samples and filled symbols inner-crown samples. Lines indicate linear or piecewise regressions. Solid lines denote significant ($P < 0.05$) and broken lines denote insignificant relationships



Mass-based P_{max} decreased linearly with increasing height (Fig. 6a). In contrast, the highest area-based P_{max} was observed at mid-heights (70–90 m) for five of the seven trees measured (Fig. 6b). A quadratic fit of the pooled data indicated that maximum area-based P_{max} occurred at 78.4 m. Mass-based P_{max} decreased linearly with increasing SMA (Fig. 6c). In contrast, area-based P_{max} increased with increasing SMA in the lower crown (Fig. 6d, $R^2 = 0.482$, $P = 0.012$) but was not correlated with SMA in the upper crown ($R^2 = 0.002$, $P = 0.889$).

Discussion

Hydrostatic constraints on morphological exploitation of light

Decreasing soil water supply and increasing demand due to evapotranspiration from leaves resulted in lower Ψ during the dry than wet season and at midday than at predawn. The vertical gradient in Ψ of the ten study trees generally conformed to the theoretical hydrostatic gradient. In our study trees, leaves 100 m above the ground were subjected to average Ψ of -1.08 and -1.35 MPa at predawn and midday during the wet season, respectively. These values decreased to -1.23 and -1.71 MPa during the dry season. Decreasing leaf water potential with increasing height and

diurnal water loss contribute to greater water stress at the treetop, especially during the dry season when midday xylem pressures approach the cavitation threshold in *S. sempervirens* (i.e., -1.9 MPa, Koch et al. 2004).

Increasing SMA and $\delta^{13}\text{C}$ with increasing height indicated decreasing shoot surface area and increasing photosynthetic water use efficiency (PWUE), respectively, toward the tree top. In contrast to the continuous changes observed in relation to height, morphological and physiological characteristics did not correspond to the exponential increase in light availability with increasing height. This suggests that shoot morphology and PWUE are not determined by light environment in the upper crown.

Young, vigorously growing conifer trees generally exhibit excurrent crown form where greater shoot elongation and dry mass production occur in the upper than in the lower crown (Kozłowski and Ward 1961; Ford et al. 1987; Powell 1988). For example, in *Picea abies* (L.) Karst. and *Pinus sylvestris* L. trees up to 40 m tall, shoot length and leaf mass both increase with increasing height (Niinemets 2002). This may be an adaptive response for allocating growth to areas of the crown receiving more light. Excurrent crown form, however, is not observed in tall trees that are growth-limited. For example, measured rates of branch terminal shoot elongation in four conifer species [*P. menziesii*, *Tsuga heterophylla* (Raf.) Sarg., *Abies amabilis* (Dougl.) Forbes, *Abies grandis* (Dougl. ex. D. Don)

Fig. 3a–h Leaf and shoot morphology in relation to height for three *S. sempervirens* trees. Lines indicate significant linear or exponential regressions ($P < 0.01$). SPAR shoot silhouette area to projected leaf area ratio, LMA leaf mass per unit area; for other abbreviations, see Figs. 1 and 2

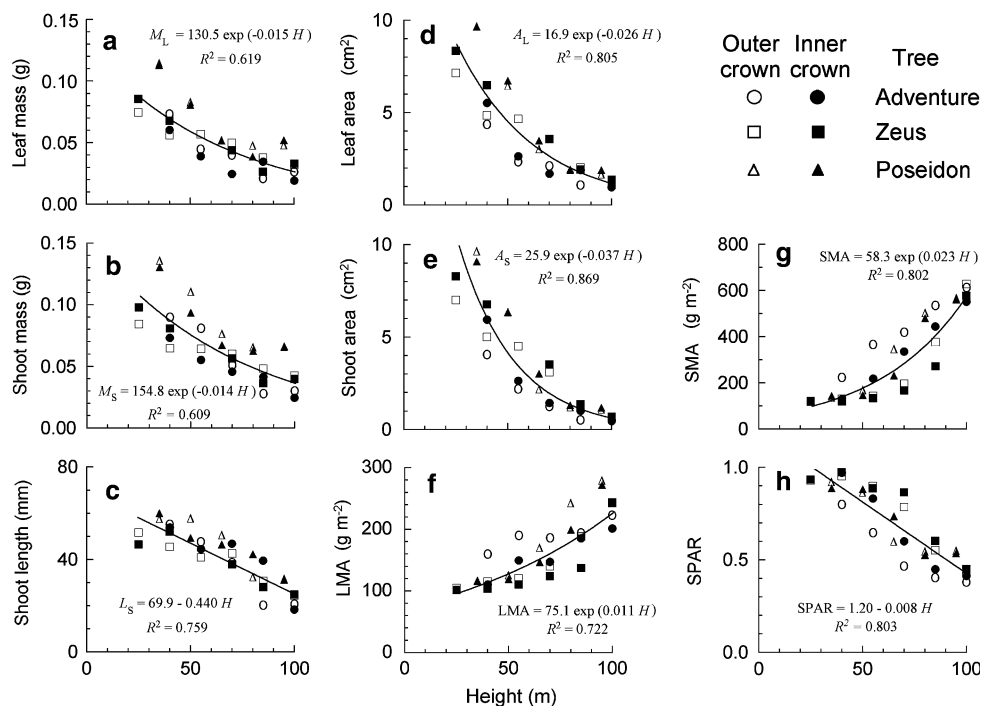
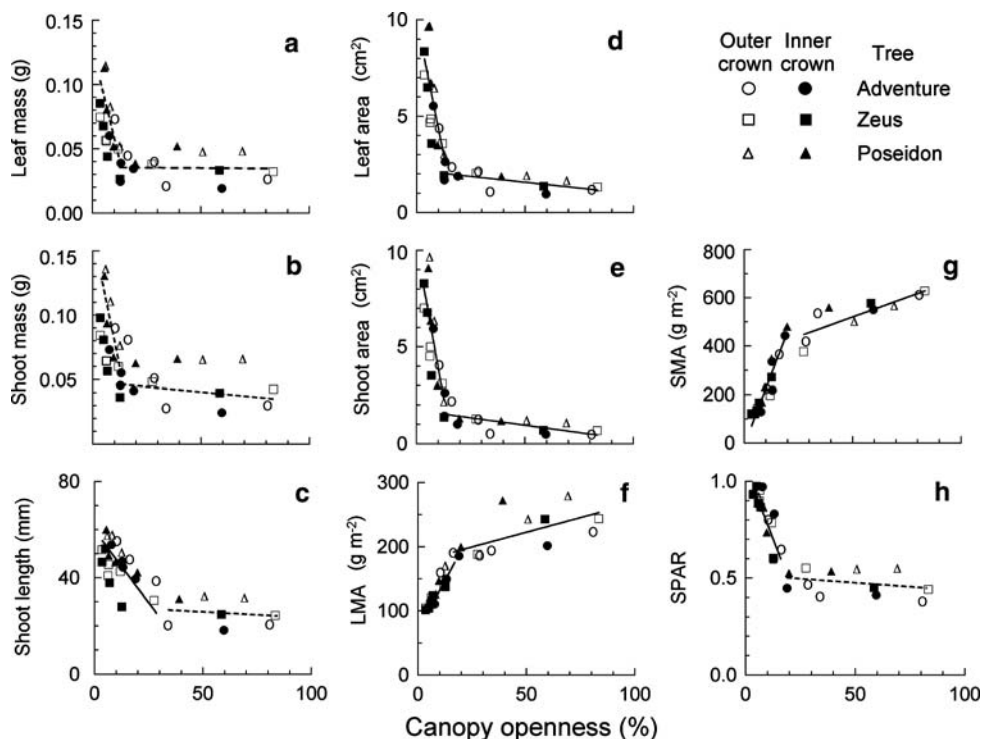


Fig. 4a–h Leaf and shoot morphology in relation to I_{CO} for the three *S. sempervirens* trees. Lines indicate the piecewise regression models (Table 3). Solid lines denote significant ($P < 0.05$) and broken lines denote insignificant relationships. For abbreviations, see Figs. 1, 2, 3

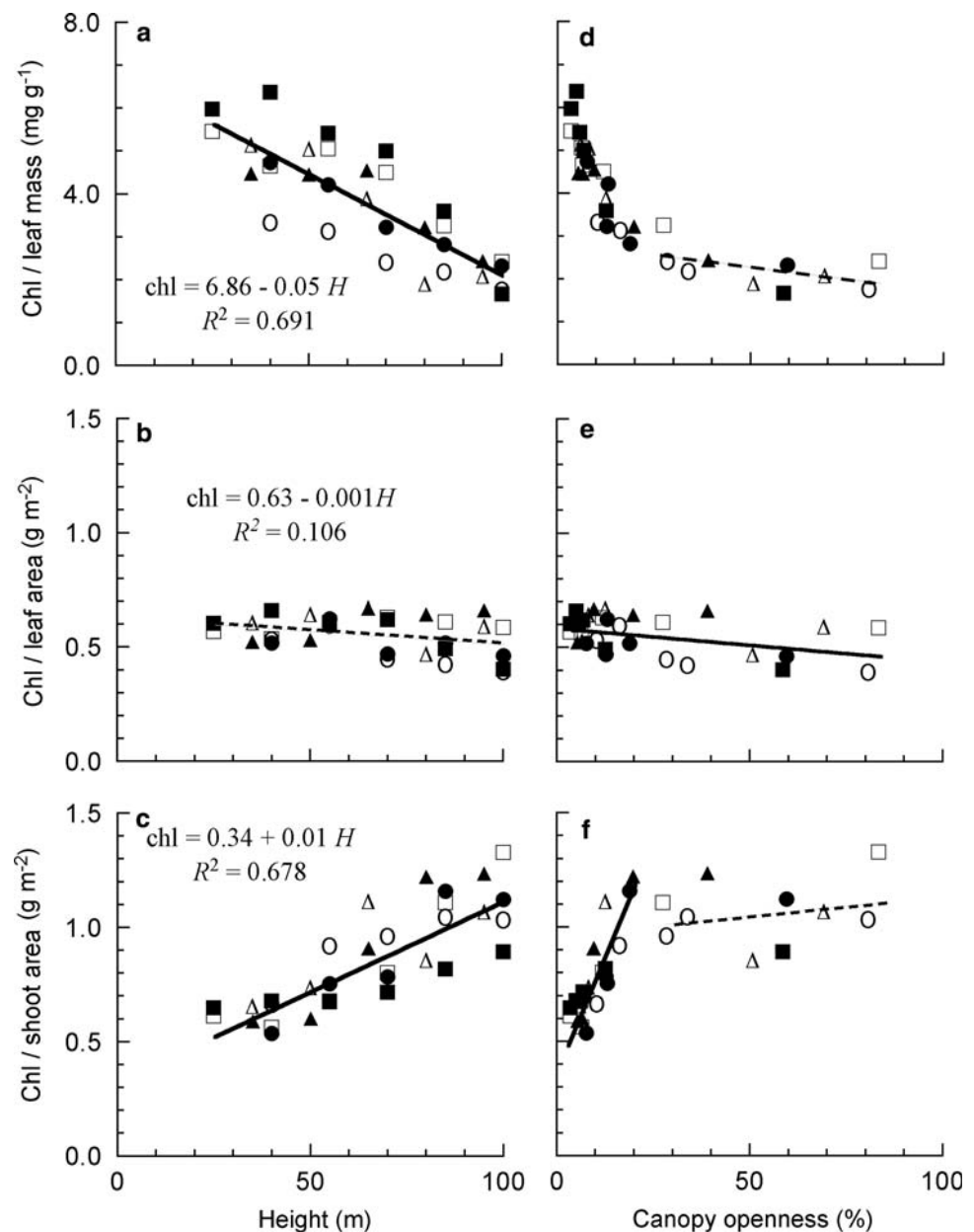


Lindl.] in an old-growth forest in western Washington indicated excurrent crown form for trees shorter than 40 m, whereas in the taller trees, shoot elongation rates were low in all parts of the crown and did not correspond to the vertical gradient in light availability (Ishii et al. 2007). Similarly, this study showed that, in tall *S. sempervirens* trees, shoot size does not increase despite marked increases

in light availability in the upper crown. This suggests that shoot elongation and dry mass production in the upper crown are not determined by light environment, because they may be constrained by hydrostatic limitation.

As with shoot and leaf mass, shoot silhouette area of many coniferous trees increases with increasing light availability in short, young trees (e.g., 3- to 4-m-tall,

Fig. 5a–f Chlorophyll concentration of leaves in relation to height and I_{CO} for the three *S. sempervirens* trees. Symbols and lines are as in Figs. 3 and 4



35-year-old *A. amabilis* trees, Sprugel et al. 1996). By contrast, in tall *S. sempervirens* trees, both shoot area and leaf area decreased with increasing height and light availability. In the upper crown, however, both shoot area and leaf area changed very little despite the marked increase in light availability. In trees up to 60 m tall, measures of light interception efficiency (LMA, SMA, and SPAR) change continuously with increasing light availability (e.g., Niinemets and Kull 1995b; Thomas and Winner 2002). With increasing height, LMA and SMA both increase as leaf thickness and twig thickness increase, and SPAR decreases as leaf overlap within shoots increases. In many cases, the morphological response is nonlinear, such that the rate of change is less at higher values of light availability (e.g.,

Stenberg et al. 1998; Niinemets 2005). This curvilinear response has been attributed to the hyperbolic decline in hydraulic conductance with increasing height (Niinemets 2002). In tall *S. sempervirens* trees, we observed marked changes in LMA, SMA, and SPAR with increasing I_{CO} in the lower crown, but these measures of light interception efficiency did not correspond to light availability in the upper crown. Both leaf and shoot morphology continue to change in the upper crown, but these changes seem to have no effect on light interception.

Our results suggest that light environment determines morphological characteristics of leaves and shoots in the lower crown of tall *S. sempervirens* trees. Although morphological and physiological characteristics were not

Table 3 Regression equations for leaf and shoot morphology and chlorophyll concentration in relation to canopy openness (I_{CO}) for three *S. sempervirens* trees studied in northern California. R^2 -values in parentheses denote insignificant relationships ($P > 0.05$). M_L leaf mass (mg), M_S shoot mass (mg), L_S shoot length (mm), A_L projected leaf area (cm^2), A_S shoot silhouette area (cm^2), LMA M_L/A_L (g m^{-2}),

SMA M_S/A_S (g m^{-2}), $SPAR$ A_S/A_L , chl/M_L chlorophyll content per leaf mass (mg g^{-1}), chl/A_L chlorophyll content per projected leaf area (g m^{-2}), chl/A_S chlorophyll content per shoot silhouette area (g m^{-2}), q point of transition of the piecewise regression, H_{crit} height (m) below which I_{CO} greater than q was not observed in the study trees

Dependent variable	Regression equation	q	R^2	H_{crit}
M_L	$\begin{cases} M_L = 130.01 - 7.03I_{CO} \\ M_L = 35.55 - 0.011I_{CO} \end{cases}$	12.6	(0.207) (0.001)	55
M_S	$\begin{cases} M_S = 153.2 - 8.05I_{CO} \\ M_S = 58.83 - 2.12I_{CO} \end{cases}$	12.6	(0.210) (0.099)	55
L_S	$\begin{cases} L_S = 59.86 - 1.206I_{CO} \\ L_S = 28.52 - 0.050I_{CO} \end{cases}$	29.0	0.326 (0.023)	85
A_L	$\begin{cases} A_L = 9.95 - 0.562I_{CO} \\ A_L = 2.21 - 0.012I_{CO} \end{cases}$	12.6	0.501 0.410	55
A_S	$\begin{cases} A_S = 10.25 - 0.628I_{CO} \\ A_S = 1.76 - 0.015I_{CO} \end{cases}$	12.6	0.573 0.420	55
LMA	$\begin{cases} LMA = 76.50 - 6.25I_{CO} \\ LMA = 177.9 - 0.91I_{CO} \end{cases}$	15.2	0.753 0.393	70
SMA	$\begin{cases} SMA = -5.95 - 23.39I_{CO} \\ SMA = 361.3 - 3.24I_{CO} \end{cases}$	20.0	0.893 0.698	70
SPAR	$\begin{cases} SPAR = 1.08 - 0.029I_{CO} \\ SPAR = 0.516 - 0.001I_{CO} \end{cases}$	16.3	0.714 (0.087)	70
chl/M_L	NA ^a	27.5 ^b	–	70 ^b
chl/A_L	$Chl = 0.592 - 0.0015 I_{CO}$	–	0.174	–
chl/A_S	$\begin{cases} Chl = 0.357 - 0.041I_{CO} \\ Chl = 0.002 - 0.974I_{CO} \end{cases}$	25.9	0.709 (0.062)	70

^a NA indicates that the piecewise regression model did not converge (q could not be estimated)

^b H_{crit} for chl/M_L was determined based on the lowest observed I_{CO} above which chl/M_L showed no correlation with I_{CO} (see Fig. 5)

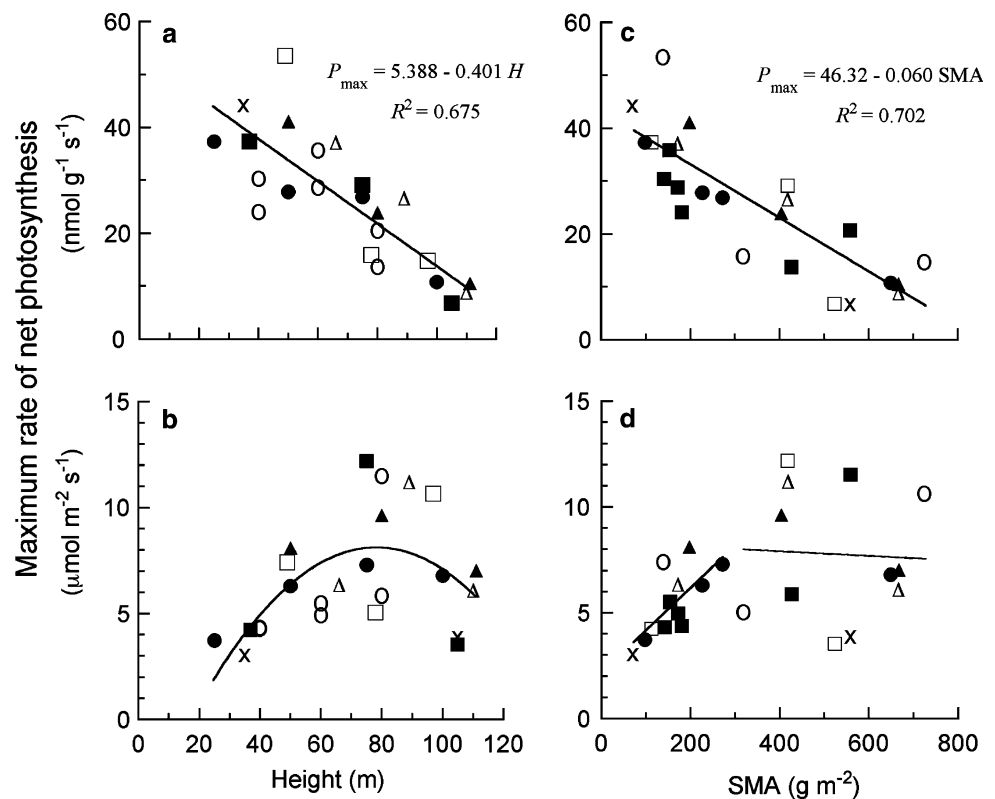
correlated with light availability in the mid-height ranges (Fig. 4), both LMA and SMA were higher and mass-based chl concentration was lower for outer- than inner-crown positions (Figs. 3f, g, 5a, respectively), suggesting some local effect of light availability remains. In the upper crown, however, hydrostatic limitation becomes the dominating factor controlling leaf and shoot morphology. This suggests that while lower-crown shoots show morphological characteristics adapted to low irradiance, hydrostatic limitation constrains morphological development, such that shoots in the upper crown are unable to fully exploit the favorable light environment.

Effects of height-induced morphological constraints on photosynthetic capacity

Compared to short trees, mass-based photosynthetic capacity of tall trees is lower, whereas area-based photosynthetic capacity is higher (e.g., Kull and Koppel 1987 for *Picea abies*; Thomas and Winner 2002 for *Pseudotsuga menziesii* and *T. heterophylla*). Similarly, within the crowns of tall trees, mass-based photosynthetic capacity

decreases with increasing height (Koch et al. 2004, *S. sempervirens*), whereas area-based photosynthetic capacity increases (Lewis et al. 2000, *P. menziesii* and *T. heterophylla*). These apparently contradicting height-related trends in photosynthetic capacity have been attributed to increasing LMA with increasing height. Thus, changes in LMA and related aspects of leaf morphology are critical to understanding changes in photosynthetic capacity with increasing tree size (Thomas and Winner 2002; Vanderklein et al. 2007), but the pattern of increasing area-based photosynthetic capacity with height is inconsistent among species. Both mass- and area-based photosynthetic capacity decrease with increasing height in 40-m-tall *Picea abies* and *Pinus sylvestris* trees, despite increases in LMA (Niinemets 2002). This implies that morphological acclimation to high irradiance may be constrained in tall trees. In our study, area-based P_{max} peaked around 80 m and then decreased toward the upper crown. In the upper crown, both LMA and SMA showed reduced responses to increasing light availability, and area-based P_{max} was not correlated with SMA. These results suggest that hydrostatic constraints on morphological development may restrict

Fig. 6a–d Light-saturated maximum rate of net photosynthesis in relation to height and SMA for the six *S. sempervirens* trees. Symbol shapes indicate different trees. Solid lines denote significant ($P < 0.05$) and broken lines denote insignificant relationships



morphological acclimation to increasing light availability in the upper crown of tall *S. sempervirens* trees and contribute to reduced area-based photosynthetic capacity.

Decreasing mass-based photosynthetic capacity with increasing height indicates lower photosynthetic C gain relative to dry mass investment in foliage (Köstner et al. 2002; Niinemets 2005). Hydrostatic limitation constrains shoot elongation and leaf expansion in *S. sempervirens* and other tall conifers (Koch et al. 2004; Woodruff et al. 2004). Anatomical and physiological changes associated with such morphological reductions in leaves (e.g., increased tissue density, mesophyll resistance to CO₂ diffusion, and rate of leaf respiration: Parkhurst 1994; Niinemets 1999; Koch et al. 2004; Vanderklein et al. 2007), as well as the osmotic adjustments necessary to maintain sufficient turgor during shoot development (Woodruff et al. 2004), probably exacerbate the negative effect of reduced stomatal conductance on photosynthetic capacity in tall trees. Our results suggest that, in addition to stomatal limitation of photosynthesis, morphological and biochemical limitations may be important factors that contribute to reduced photosynthetic rates in tall trees.

Integrated response of hydraulics, morphology, and photosynthesis to increasing height

Reduced stomatal conductance is a prominent response to increasing water stress with increasing height, and stomatal

limitation of photosynthesis is a central postulate of the hydraulic limitation hypothesis (Ryan et al. 2006). Reduced stomatal conductance of tall trees, however, does not fully account for reductions in photosynthesis and growth. Theoretical studies suggest that if the objective is to maximize C gain, the ratio of leaf area to sapwood area should increase with increasing height because allocation to photosynthetic capacity is favored over sustaining stomatal conductance (Buckley and Roberts 2005). This contradicts predictions of decreasing leaf area to sapwood area ratio for maintaining stomatal conductance and hydraulic homeostasis. In addition, the hydraulic limitation hypothesis did not consider any role of structural and anatomical changes with increasing tree size.

Our results showed that above 70–80 m, both light interception efficiency and photosynthetic capacity did not correspond to increasing light availability in tall *S. sempervirens* trees. Increasing LMA and SMA mitigate reductions in leaf-specific hydraulic conductivity (Niinemets 2002; Burgess et al. 2006). In tall coniferous trees, LMA increases with increasing height in the crown, sometimes independent of changes in light availability (e.g., Ishii et al. 2002; Marshall and Monserud 2003; Koch et al. 2004) suggesting that, in tall trees, vertical changes in leaf morphology may be hydraulically controlled. Hydraulic constraints may be an important factor determining the observed vertical gradient in leaf and shoot morphology of tall *S. sempervirens* trees, especially in the

upper crown where morphological development may be constrained by the hydrostatic gradient. Newly emerging evidence suggests that limitations on anatomical development may lead to constraints on the pattern on C allocation (i.e., sink limitation, Ryan et al. 2006). Future studies should consider interactions among hydraulic, structural, anatomical, and biochemical properties in response to increasing height in order to elucidate the integrated physiological mechanism that leads to reductions in growth rate with increasing tree height.

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