

Pushing the limits to tree height: could foliar water storage compensate for hydraulic constraints in *Sequoia sempervirens*?

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Summary

1. The constraint on vertical water transport is considered an important factor limiting height growth and maximum attainable height of trees. Here, we show evidence of foliar water storage as a mechanism that could partially compensate for this constraint in *Sequoia sempervirens*, the tallest species.

2. We measured hydraulic and morpho-anatomical characteristics of foliated shoots of tall *S. sempervirens* trees near the wet, northern and dry, southern limits of its geographic distribution in California, USA.

3. The ability to store water (hydraulic capacitance) and saturated water content (leaf succulence) of foliage both increased with height and light availability, maintaining tolerance of leaves to water stress (bulk-leaf water potential at turgor loss) constant relative to height.

4. Transverse-sectional area of water-storing, transfusion tissue in leaves increased with height, while the area of xylem tissue decreased, indicating increasing allocation to water storage and decreasing reliance on water transport from roots.

5. Treetop leaves of *S. sempervirens* absorb moisture via leaf surfaces and have potential to store more than five times the daily transpirational demand. Thus, foliar water storage may be an important adaptation that helps maintain physiological function of treetop leaves and hydraulic status of the crown, allowing this species to partially compensate for hydraulic constraints and sustain turgor for both photosynthesis and height growth.

Key-words: height growth, hydraulic limitation, leaf anatomy, leaf capacitance, leaf succulence, water relations

Introduction

Sequoia sempervirens is the only tree species with living individuals exceeding 100 m in height. The tallest living individual was remeasured at 115.76 m in 2013 (S.C. Sillett unpublished). The physiological mechanisms underlying its incredible height have recently been documented (Koch *et al.* 2004; Ishii *et al.* 2008). Water supply to treetop leaves is a key factor determining maximum attainable tree height in *S. sempervirens* (Ambrose, Sillett & Dawson 2009) and other tall species (Ryan, Phillips & Bond 2006; Meinzer *et al.* 2010). With increasing height, both the distance from roots to leaves and the hydrostatic gradient caused by gravity impose limits on water transport (Midgley 2003). Thus, treetop leaves operate under some mini-

mum constant water stress, constraining important physiological functions, including cell elongation and photosynthesis, and ultimately limiting height growth (Mencuccini *et al.* 2005; Ryan, Phillips & Bond 2006). Due to these constraints, the estimated maximum attainable height for *S. sempervirens* under current environmental conditions is at least 122 m (Koch *et al.* 2004; Koch & Sillett 2009). In addition to a limited water supply, drier air and higher temperatures near the treetop caused by high light intensities increase evaporative demand, exacerbating leaf water stress (Franks 2006). This is an inescapable consequence of height, and tall trees must cope with the dilemma that water stress is never alleviated and greatest where light availability for photosynthesis is highest.

The incredible stature of *S. sempervirens* suggests this species may have physiological adaptations that compensate for increasing water stress with height (West, Brown & Enquist 1999; Du *et al.* 2008), which may include

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reduction of water stress by absorption of moisture through leaf surfaces (Burgess & Dawson 2004). The tallest individuals occur in moist temperate forests near the species' northern distribution limit in California, where rainfall is abundant and summer fog occurs frequently (Dawson 1998). In contrast, tree heights are lower in drier regions near the species' southern distribution limit. Absorption of fog via leaf surfaces reduces water stress of *S. sempervirens* leaves, so that leaf water supply does not depend solely on soil water availability and transport from roots (Simonin, Santiago & Dawson 2009). If the absorbed water can be stored in treetop leaves, it would reduce further the reliance on vertical water transport. Although hydraulic capacitance of woody tissue is considered an important internal source of water in large trees (Phillips *et al.* 2003; Cermak *et al.* 2007; Scholz *et al.* 2011), foliar water storage has received less attention (Sack *et al.* 2003).

A striking feature of *S. sempervirens* is the great variation in shoot/leaf morphology from top to bottom of the crown, which can span more than 90 m in depth (Koch *et al.* 2004). Treetop leaves are small, thick and fused to the vertically oriented shoot axis. In contrast, lower-crown leaves are large, flat and segregated from the horizontally oriented shoot axis. Generally, acclimation to the vertical gradient in light availability explains changes in leaf morphology within a tree crown (Valladares & Niinemets 2007; Niinemets 2010). In tall trees, however, morpho-anatomical characteristics of leaves are more strongly determined by hydraulic properties associated with height (Marshall & Monserud 2003; Cavaleri *et al.* 2010; Oldham *et al.* 2010). In tall *S. sempervirens*, leaf mass per area (LMA) increases with height, leading to less evaporative

surface area per unit leaf mass, whereas LMA is not correlated with light intensity above 70 m (Ishii *et al.* 2008). Leaves of all gymnosperm species have water-storing, transfusion tissue surrounding vascular bundles (Brodrribb & Holbrook 2005; Aloni, Foster & Mattsson 2013). Transfusion tissue, first documented in 1864, is a tracheary element composed of tracheids, parenchyma and albuminous cells (Takeda 1913; Hu & Yao 1981). In *S. sempervirens*, the amount of transfusion tissue increases with increasing height, reflecting anatomical acclimation to increasing water stress (Oldham *et al.* 2010).

In this study, we measured the hydraulic and morpho-anatomical characteristics of leaves of tall *S. sempervirens* trees near the wet, northern and dry, southern limits of its distribution in California. We investigate how the capacity and mechanisms for foliar water storage respond to increasing water stress associated with increasing height and atmospheric evaporative demand. We discuss how such adaptations may contribute to maintaining hydraulic status in treetop leaves of the world's tallest species.

Materials and methods

The study was conducted at Prairie Creek Redwoods State Park (41.37°N, 124.02°W, 55 m asl) and Landels-Hill Big Creek Reserve (36.05°N 121.57°W, 60 m asl). Long-term (1895–2012) average annual precipitation at Prairie Creek is 1857 mm with 55 mm occurring during summer months (June, July and August), whereas Landels-Hill receives 801 mm with only 5 mm occurring in summer (PRISM Climate Group 2013). Based on records from Arcata Airport (40.98°N, 124.11°W, 64 m asl) and Monterey Peninsula Airport, CA (36.58°N, 121.85°W, 50 m asl) located near the two study sites, long-term (1951–2009) averages of fog

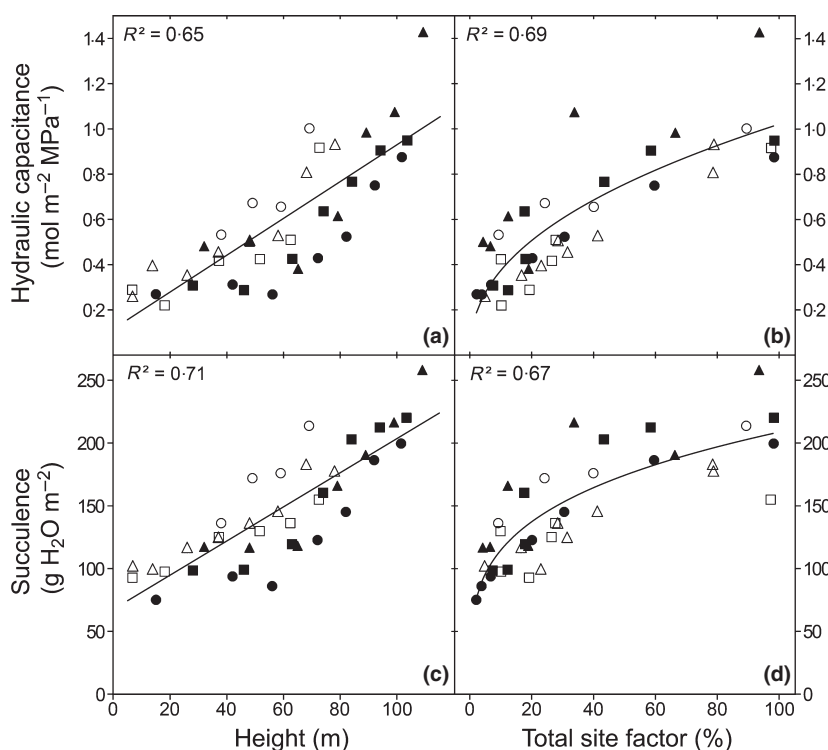


Fig. 1. Water storage of small, foliated shoots of tall *S. sempervirens* trees. Hydraulic capacitance (a, b) and succulence (saturated water content per leaf surface area (c, d)) shown in relation to height and light availability (total site factor). Each datum represents mean of three to five foliated shoots sampled at each height. Filled and open symbols denote trees in Prairie Creek Redwoods State Park and Landels-Hill Big Creek Reserve, respectively. Symbol shapes denote different trees. Regression lines fitted to data from all six trees.

frequencies (i.e. number of days when visibility <1 km) are 43.5 and 40.5%, respectively, with fog frequencies being highest during summer months (Johnstone & Dawson 2010).

We selected three study trees from among the tallest individuals at each site. Heights of the study trees were 109.9, 103.9 and 101.9 m at Prairie Creek and 79.8, 72.9 and 70.0 m at Landels-Hill. We climbed trees using ropes and stretched a tape measure from treetop to ground level. Small branches (30–50 cm long) were sampled from the outer crown of each tree at 10- to 15-m intervals from just below treetop to the lowest living branch. Hemispherical photographs were taken directly above each sampling location to quantify the light environment. Sample branches were sealed in black plastic bags, transported to the ground, immediately recut under water and fully rehydrated in the laboratory overnight.

We used the bench-drying approach to the pressure–volume technique (Tyree & Hammel 1972; Schulte & Hinckley 1985) to measure bulk-leaf water potential (Ψ_L) and fresh weight (before and after each water potential reading) repeatedly of three to five small, foliated shoots comprising second- and current-year internodes (repeat pressurization method, Hinckley *et al.* 1980; Ritchie & Roden 1985; Parker & Colombo 1995). Care was taken to increase and decrease the pressure in the chamber very slowly (<0.01 MPa s⁻¹) so as not to damage the sample shoot. During our pressure–volume measurements, when the shoot was slowly pressurized to force water out of the xylem, we observed cases where excess water (i.e. water stored outside of vascular tissue) entered the xylem and bulk-leaf water potential recovered. We corrected for this effect following methods described in (Kubiske & Abrams 1991).

The pressure–volume curve was used to calculate fresh weight at saturation (M_F , g), hydraulic capacitance (C , mol m⁻² MPa⁻¹), osmotic potential at turgor loss (Ψ_{tip} , MPa) and relative water content at turgor loss (RWC_{tip}) at the bulk-shoot level (Cheung, Tyree & Dainty 1975; Richter 1978; Tyree & Richter 1981; Schulte & Hinckley 1985). To calculate C , we first estimated Ψ_{tip} from the inflection point of the Ψ_L –RWC relationship. The slope of the relationship before turgor loss was multiplied by the saturated water content (mol H₂O) of the shoot and divided (normalized) by total leaf surface area (A_L) (Brodribb *et al.* 2005). To quantify the maximum amount of foliar water storage, we calculated bulk-shoot succulence (S , g H₂O m⁻²), which is defined as $(M_F - M_D)/A_L$, where M_D is dry mass (g) of the foliated shoot (Bacelar *et al.* 2004). C represents the ability of shoots to store water relative to transpiring leaf area, while S represents the maximum amount of water that can be stored. In the process of calculating C , the bulk tissue elastic modulus was also calculated. Because C is standardized by leaf area, it provides an adequate relative measure of cell-wall elasticity.

To quantify shoot silhouette area (A_S), we scanned sample shoots at 600 dpi using a flatbed scanner (Expression 10000XL, Epson America Inc., Long Beach, CA, USA). All leaves were then removed from the shoot axis, placed on the scanner with no overlap and scanned to quantify projected leaf area (A_P). To observe leaf anatomy, second-year leaves were fixed in FPA, transversely sectioned at mid-point to 20 μ m thickness using a microtome and double stained with safranin and fast green. Photographed images (400 \times magnification) of the transverse leaf sections were used for anatomical analyses. All shoot samples were oven-dried at 70 °C to constant weight to determine M_D .

DATA ANALYSES

We analysed hemispherical photographs using Gap Light Analyzer (ver 3.1, Simon Fraser University, Burnaby, BC, Canada) to calculate canopy openness, total radiation simulated over a 12-month growing season and three site factors expressing the percentage of

direct, indirect and total radiation received. Total site factor (hereafter TSF) was most strongly correlated with hydraulic and morphological variables and therefore used as the measure of light availability. Scanned images of shoots and leaves were analysed using Image J (National Institutes of Health, Bethesda, MD, USA) to determine A_S and A_P . We calculated leaf mass per area (LMA, g m⁻²) as the ratio of leaf dry mass to A_P and shoot mass per area (SMA, g m⁻²) as the ratio of M_D to A_S . Perimeter-to-width ratios of leaf transverse sections were multiplied by A_P to obtain A_L (Barclay & Goodman 2000), which was then used to calculate C . All hydraulic and morphological variables were regressed against height and TSF using model fitting in JMP 10 (SAS Institute Inc.). The difference between sites was examined via analysis of covariance (separate slopes model) with height and TSF as covariates.

Results

Both hydraulic capacitance (C) and leaf succulence (S) of foliated shoots increased with height (Fig. 1a,c, $C = (0.115 \pm 0.062) + (0.00816 \pm 0.00096)h$, $P < 0.00001$;

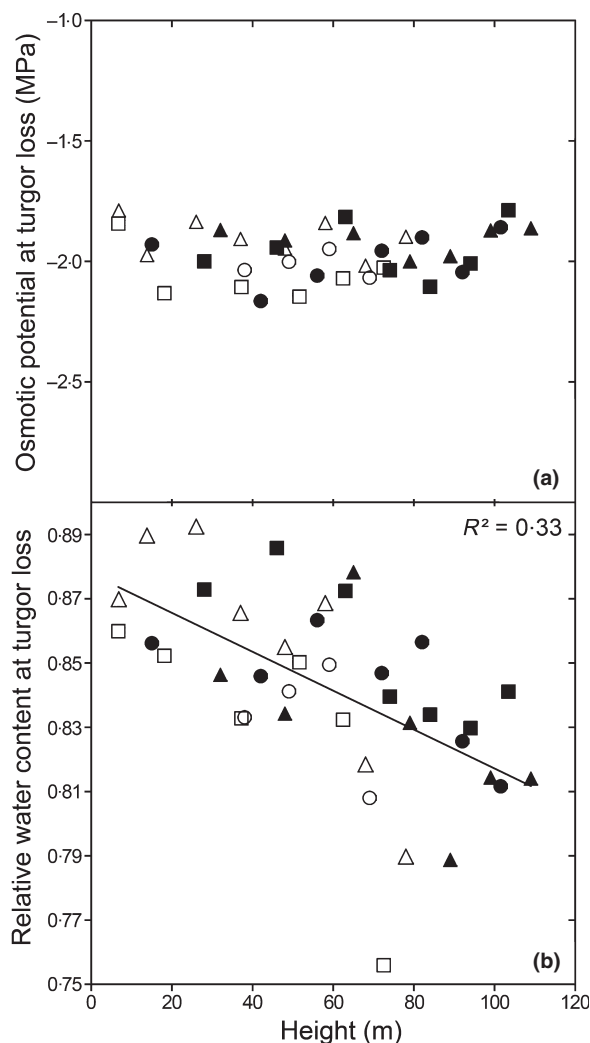


Fig. 2. Hydraulic properties of foliated shoots of tall *S. sempervirens* trees. Bulk-leaf water potential at turgor loss (a) and relative water content at turgor loss (b) shown in relation to height. Symbols and regression line as in Fig. 1.

$S = (67.7 \pm 9.1) + (1.36 \pm 0.14)h$, $P < 0.00001$, where h equals height, $n = 39$). At the same height, both C and S were greater for southern than northern trees (ANCOVA, $F = 12.69$, $P = 0.0011$ and $F = 8.93$, $P = 0.0051$, respectively). However, in relation to total site factor (TSF), there was no distinction between sites (Fig. 1b,d, $C = (0.139 \pm 0.028)TSF^{(0.434 \pm 0.051)}$, $P < 0.00001$; $S = (63.0 \pm 7.3)TSF^{(0.260 \pm 0.031)}$, $P < 0.00001$, $n = 39$). Thus, despite their lower stature (70–80 m), the highest, most exposed leaves of the southern trees had similar water storage capacity as those of the northern trees (>100 m).

In contrast, osmotic potential at turgor loss (Ψ_{tlp}) did not change with height (Fig. 2a, $\Psi_{tlp} = -1.972 \pm 0.038$, $P = 0.800$, $n = 39$). Treetop shoots had greater water storage and consequently higher water content at saturation compared to those lower in the crown. This added buffer resulted in lower relative water content at turgor loss (RWC_{tlp}) such that treetop shoots did not lose turgor until they had lost nearly 20% of their saturated water content (Fig. 2b, $RWC_{tlp} = (0.878 \pm 0.009) + (-0.00061 \pm 0.00014)h$, $P = 0.00001$, $n = 39$).

Vertical changes in leaf and shoot morphology (LMA and SMA, respectively) closely paralleled those of water storage (Fig. 3). In the northern trees, shoot morphology did not change below $c. 60$ m, where light availability was consistently low ($6.1 \pm 1.2\%$ TSF, $n = 7$), resulting in a nonlinear response. We also found anatomical changes reflecting adaptation for water storage. Transverse-sectional area of transfusion tissue (A_T) increased, whereas area of xylem tissue (A_X) decreased with height (Fig. 4a,b,

$A_T = (3.40 \times 10^{-3} \pm 1.53 \times 10^{-3}) + (1.40 \times 10^{-4} \pm 2.35 \times 10^{-5})h$, $P < 0.0001$; $A_X = (2.06 \times 10^{-3} \pm 1.16 \times 10^{-4}) - (1.10 \times 10^{-5} \pm 1.77 \times 10^{-6})h$, $P < 0.0001$, $n = 38$). The decrease in A_X with height was attributable to a decrease in the number of xylem tracheids (N_T) (Fig. 4c, $N_T = (38.51 \pm 1.93) - (0.210 \pm 0.030)h$, $P < 0.0001$, $n = 38$) as transverse-sectional area of individual xylem tracheids (a_T) did not change with height (Fig. 4d, $a_T = (54.04 \pm 2.48) + (0.018 \pm 0.038)h$, $P = 0.644$, $n = 38$).

Discussion

The structure and orientation of well-illuminated *S. sempervirens* leaves allow them to collect moisture (Fig. 5) and absorb it (Burgess & Dawson 2004; Simonin, Santiago & Dawson 2009). Our results demonstrate that some of this water can be stored internally, which could reduce reliance on water transport from roots. Foliar water uptake and storage have positive effects on physiological function in water-stressed plants (e.g. Martin & Willert 2000; Breshears *et al.* 2008). The ability of *S. sempervirens* foliage to store water increases with both height and light availability such that treetop shoots have maximum hydraulic capacitance and succulence. Compared to those lower in the crown, treetop shoots experience greater hydrostatic and hydrodynamic constraints on their internal water supply. Foliar water storage helps explain why, despite being the tallest species, midday xylem pressures in treetop shoots of *S. sempervirens* are not as low as in other tall species

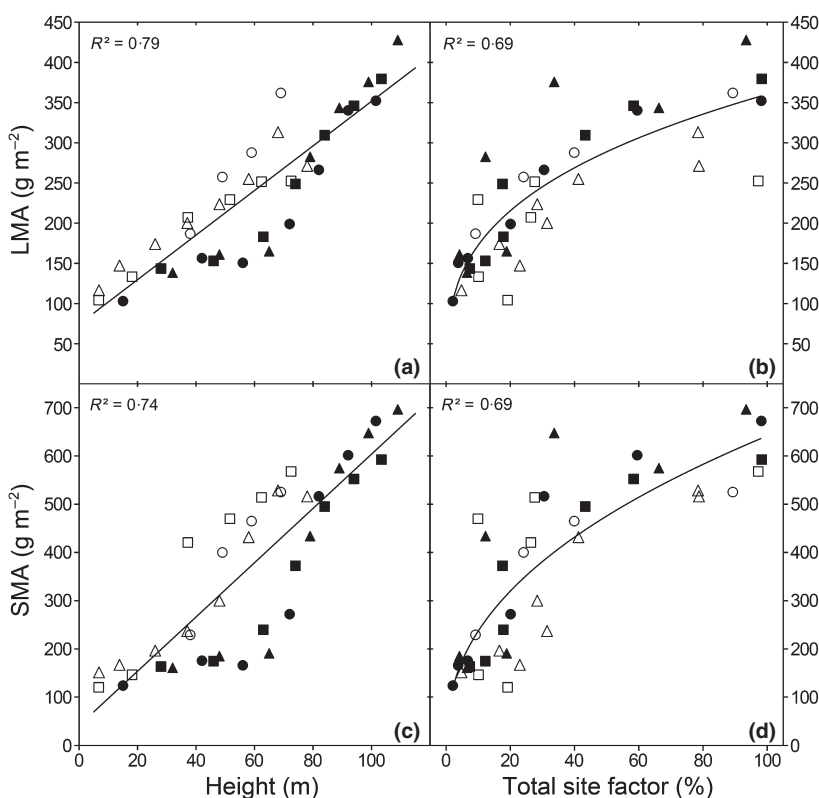


Fig. 3. Shoot/leaf morphology of tall *S. sempervirens* trees. Leaf mass per area (LMA) and shoot mass per area (SMA) shown in relation to height and light availability (total site factor). Symbols and regression lines as in Fig. 1.

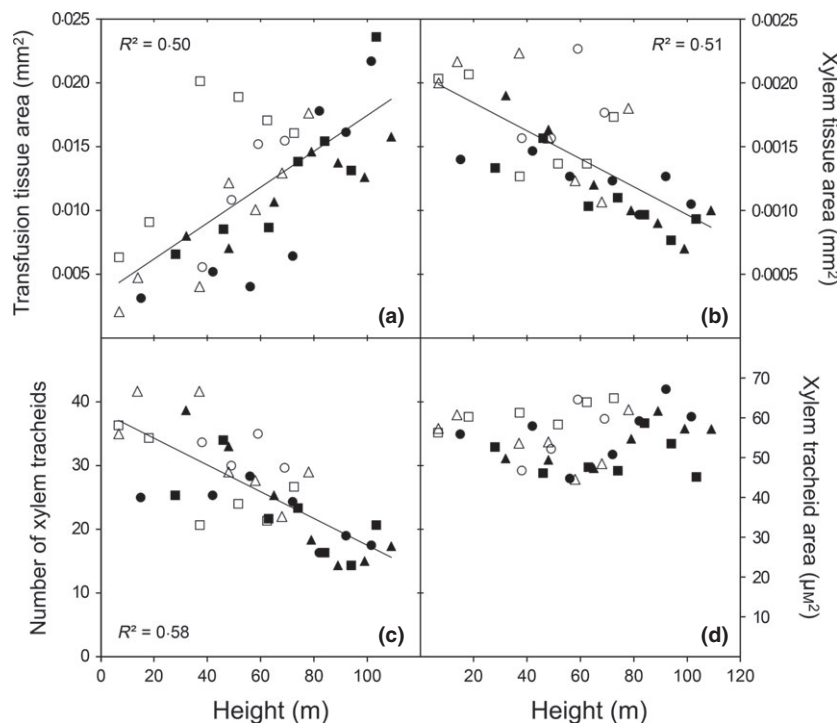


Fig. 4. Leaf anatomy of tall *S. sempervirens* trees. Transverse-sectional area of transfusion tissue (a) and of xylem (b), number of tracheids (c) and transverse-sectional area of individual tracheids (d) shown in relation to height. Symbols and regression lines as in Fig. 1.

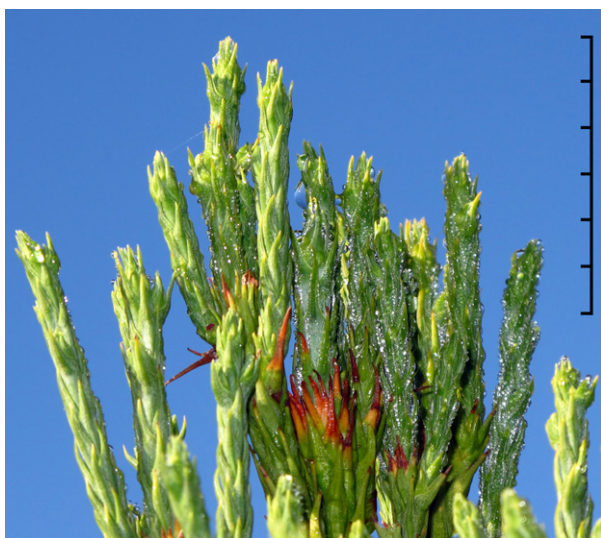


Fig. 5. Treetop leaves of the tallest *S. sempervirens* (115.72 m in 2012 when photograph was taken) still retain dew droplets on leaf surfaces by mid-morning. Scale on right indicates 6 cm of vertical growth since 2011.

(Koch *et al.* 2004; Ishii *et al.* 2008), which tolerate increasing water stress with height by reaching lower daytime water potentials and turgor loss points (Bauerle *et al.* 1999; Woodruff, Bond & Meinzer 2004). Foliar water storage is also consistent with the occurrence of xylem flow reversal in treetop branches of *S. sempervirens* (Burgess & Dawson 2004).

The mean daytime transpiration rate documented for *S. sempervirens* treetops (*c.* $0.06 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$; Ambrose *et al.* 2010) multiplied over a 10-h daytime period

amounts to $38.9 \text{ g H}_2\text{O m}^{-2}$. Thus, given the mean succulence we documented for treetop shoots ($204.1 \text{ g H}_2\text{O m}^{-2}$), foliage alone can store more than five times the daily transpirational demand at the treetop. Because we removed effects of the gravitational potential gradient in our cut-rehydrate treatment, and foliage under chronic water stress cannot remain fully saturated *in situ*, our succulence calculations likely represent maximum values for foliar water storage. Nevertheless, the magnitude of foliar water storage may help treetop leaves avoid turgor loss, maintain stomatal functioning and sustain photosynthesis.

Plant leaves under increasing water stress often acclimate by lowering the turgor loss point (Pallardy 2007). In tall trees of *P. menziesii*, Ψ_{tlp} decreases with increasing height (Bauerle *et al.* 1999; Woodruff, Bond & Meinzer 2004). We found that increasing succulence and decreasing RWC_{tlp} contributed to maintaining Ψ_{tlp} constant within the crown of tall *S. sempervirens* trees. This mechanism is similar to succulent plants that utilize stored water in dry habitats (Zimmermann & Milburn 1982; Barcikowski & Nobel 1984). Our observations of xylem pressure responses to excess water during pressure–volume measurements imply that when water potential decreases, stored water can be used to prevent xylem pressures from dropping further. Independent analyses of *S. sempervirens* leaf anatomy revealed that transfusion tissue surrounding the xylem may collapse during periods of high water stress, such that water stored therein can enter xylem tracheids and provide a leaf-level hydraulic buffer against cavitation (Oldham *et al.* 2010). Increasing area of transfusion tissue relative to xylem suggests increasing dependence on stored water and decreasing reliance on water transport with increasing height.

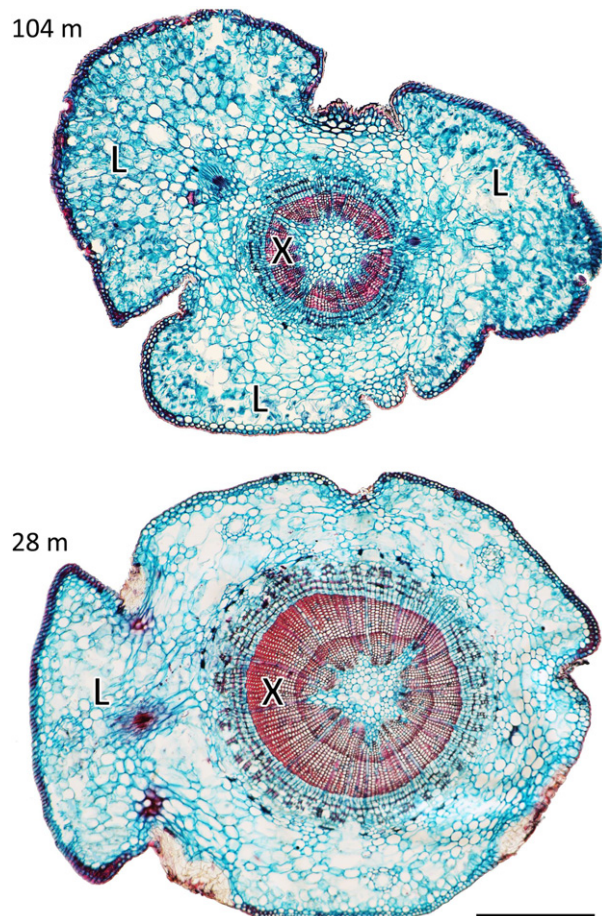


Fig. 6. Transverse-sectional anatomy of second-year foliated shoots at 104 m (top) and 28 m (bottom) in a 110-m-tall *S. sempervirens* tree. Relative area of xylem (X: stained red at centre with two annual rings) is smaller in treetop shoots whose fused stem and leaf parenchyma (L) create relatively large volume for potential water storage surrounding central conducting tissues. In contrast, leaves in lower-crown shoot are separated from stem and only leaf base is attached on left side of stem. Scale bar = 500 μ m.

In many gymnosperms, there appears to be a trade-off between xylem safety and vulnerability to cavitation such that tracheid diameters in the main stem and branches decrease with increasing height (Hacke & Sperry 2001; Tyree & Zimmermann 2002; Sperry, Meinzer & McCulloh 2008). In tall *P. menziesii* trees, both the quantity and diameter of leaf tracheids decrease with increasing height (Woodruff, Meinzer & Lachenbruch 2008). In contrast, leaf tracheid diameter was constant with respect to height in tall *S. sempervirens*. The safety margin against cavitation may be larger for stem and branches as opposed to leaves because loss of function in the former would lead to more extensive damage. Recent theoretical work suggests that xylem tapering cannot compensate completely for the hydraulic limitations of tree growth (Zaehle 2005), leaving open the possibility that other compensating mechanisms are involved. Our results indicate that anatomical changes may help maintain homeostasis of shoot hydraulic functioning in *S. sempervirens*. In the upper crown, leaves fuse

to the shoot axis creating a relatively large tissue volume and intercellular space surrounding xylem that likely stores more water per unit xylem than in the lower crown (Fig. 6). In addition to quantitative aspects of leaf and shoot anatomy, decreasing RWC_{tip} and increasing hydraulic capacitance with increasing height and light availability reflect greater cell-wall elasticity, which enhances the potential of individual cells, including transfusion tissue, to expand and store water (Brodribb *et al.* 2005).

Similar leaf- and shoot-level responses to light availability in taller northern and shorter southern forests suggest that on top of the hydrostatic gradient, which increases linearly with height, evaporative demand driven by light intensity helps determine morphological, anatomical and physiological characteristics in of *S. sempervirens* foliage. Associated with height- and light-related changes in shoot structure, various hydraulic resistances within leaves also limit photosynthesis (Sack & Holbrook 2006; Brodribb, Field & Jordan 2007; Mullin *et al.* 2009). In *S. sempervirens*, water storage near the site of photosynthesis helps overcome these constraints, explaining how the world's tallest species solves the dilemma that water stress is greatest where light availability for photosynthesis is highest.

Acknowledgements

This research was supported by the Save-the-Redwoods League, the Kenneth L. Fisher Chair in Redwood Forest Ecology at Humboldt State University, JSPS (KAKENHI #23380085 and #20780118), HUMAP and Hyogo STA. We thank the California Department of Parks and Recreation and Landels-Hill Big Creek Reserve for permission to conduct the research and M. Antoine, J. Spickler, A. Ambrose, A. Carroll, R. Kramer and E. Coonen for assistance in the field and laboratory. D. R. Woodruff, F.C. Meinzer, M.G. Ryan and C. B. Williams provided helpful comments on earlier versions of the manuscript, which was written when HRI was a visiting scholar at HSU. We dedicate this study to the memory of Greg Jennings, whose pioneering work on redwood anatomy, morphology and water relations continues to inspire our research.

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Received 26 November 2013; accepted 13 April 2014
 Handling Editor: Jenny Watling