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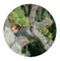

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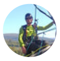

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The limits to tree height

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Trees grow tall where resources are abundant, stresses are minor, and competition for light places a premium on height growth[1,2]. The height to which trees can grow and the biophysical determinants of maximum height are poorly understood. Some models predict heights of up to 120 m in the absence of mechanical damage[3,4], but there are historical accounts of taller trees[5]. Current hypotheses of height limitation focus on increasing water transport constraints in taller trees and the resulting reductions in leaf photosynthesis[6]. We studied redwoods (*Sequoia sempervirens*), including the tallest known tree on Earth (112.7 m), in wet temperate forests of northern California. Our regression analyses of height gradients in leaf functional characteristics estimate a maximum tree height of 122–130 m barring mechanical damage, similar to the tallest recorded trees of the past. As trees grow taller, increasing leaf water stress due to gravity and path length resistance may ultimately limit leaf expansion and photosynthesis for further height growth, even with ample soil moisture.

According to the cohesion-tension theory, water transport in plants occurs along a gradient of negative pressure (tension) in the dead, tube-like cells of the xylem, with transpiration, water adhesion to cell walls, and surface tension providing the forces necessary to lift water against gravity[7]. Height growth may slow if the xylem tension and therefore leaf water potential (Ψ) predicted for great heights, $\lesssim -2$ MPa (ref. 7), reduces sufficiently the positive pressure (turgor) necessary for expansion of living cells or increases the risk of xylem cavitation—cavitation is the formation of embolisms that reduce hydraulic conductivity and can cause branch dieback and plant death[8,9]. Many trees respond to Ψ below -1 MPa by decreasing the aperture of microscopic pores (stomata) in leaves through which water vapour is lost in transpiration and carbon dioxide (CO_2) is gained in photosynthesis[10]. Reduced stomatal conductance can decrease cavitation risk and turgor loss, but it also limits photosynthesis. Thus, as trees grow taller, maintenance of favourable water status might progressively slow height growth by reducing photosynthetic carbon gain[4,6].

We accessed the crowns of redwoods to measure water stress and photosynthesis and to collect samples for laboratory analyses. Within individual trees, the xylem pressure of small, foliated branches measured during the dry season (late September to early October) was strongly correlated with height (Fig. 1a). The gradient before dawn, when transpiration was negligible, averaged -0.0096 ± 0.0007 MPa m^{-1} for five trees over 110 m tall ($R^2 > 0.97$, $P < 0.0001$), nearly identical to the hydrostatic gradient due to gravity (-0.0098 MPa m^{-1}) as predicted by the cohesion-tension theory[7]. The slope of the xylem pressure–height relationship was slightly steeper (-0.0106 ± 0.0022 MPa m^{-1}) at midday when the evaporative gradient and transpiration were high. The minimum xylem pressure (that is, maximum tension) recorded in the highest branches sampled (108 ± 1.2 m) averaged -1.84 ± 0.04 MPa. The importance of height *per se* for water potential was evident in that nearly two-thirds of the midday xylem pressure was due to gravity.

Reduced water potential due to soil drought causes a decline in the turgor of living plant cells that is necessary for cell growth and leaf expansion[11]. To determine if this also occurs as water potential declines with height, we estimated turgor at dry-season water potentials from pressure–volume measurements. Turgor (in MPa) declined linearly with height, h, as turgor $= -(0.0074 \pm 0.0004)h + (1.30 \pm 0.07)$, $n = 4$ trees, ranging from 0.93 MPa at 50 m to 0.48 MPa at 110 m. At night when xylem pressure increased, the turgor gradient was less steep, turgor $= -(0.0044 \pm 0.0023)h + (1.39 \pm 0.19)$, and turgor was 0.3–0.4 MPa higher than at midday.

Given the role of turgor in leaf expansion, its reduction with height may underlie the distinct vertical gradient in leaf structure in redwoods (Fig. 2). Leaf shape varied from large and expanded in the lower crown to small and scale-like at the treetop. We quantified this variation in terms of the leaf mass:area ratio (LMA, g m^{-2}), which increased exponentially over a fourfold range with height (Fig. 1b, LMA $= (37.1 \pm 12.3)\exp(0.0260 \pm 0.0030)h$, $0.88 \leq R^2 \leq 0.99$, $0.0001 \leq P \leq 0.003$, $n = 5$ trees). At 112 m, LMA was similar to the highest published value for terrestrial plants[12]. Height-related variation in LMA has been attributed to light level in forest canopies[13,14]. In our study trees, we found that the direct site factor (DSF), an index of direct solar radiation based on hemispherical photographs, decreased by 14% of the value at 110 m for a 10-m decrease in height. Relative to water potential, the influence of light on LMA was small, however; DSF added only 4% to the explained variation of within-crown LMA in a multiple regression analysis including DSF ($P = 0.0025$) and predawn xylem pressure ($P < 0.0001$) as independent variables (adjusted $R^2 = 0.88$, $n = 33$ samples from five redwoods over 110 m tall). The following observations (Fig. 3) also support the hypothesis that water relations are more important than light environment in determining leaf structure in redwood: (1) leaves of a 2-m-tall epiphytic redwood rooted in soil near the top of a 95-m-tall redwood were much more

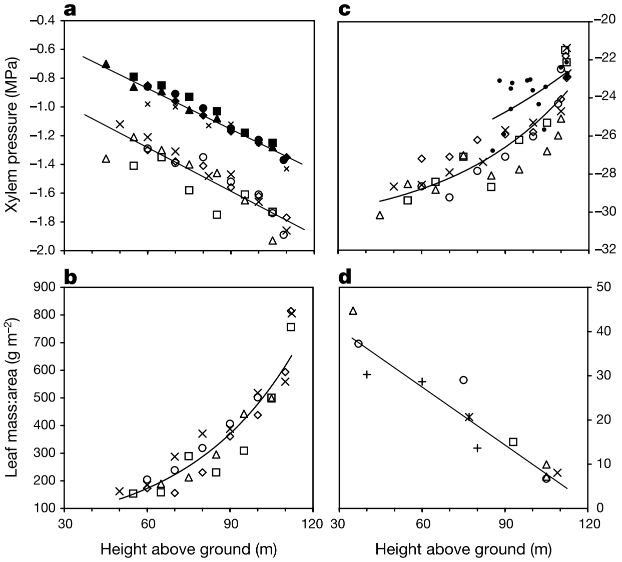

Figure 1 Variation with height in physiological and structural features of redwood trees at Humboldt Redwoods State Park, California. **a**, Xylem pressure of small branches measured at predawn (upper group) and midday (lower group) during September and October 2000. The upper line is the expected gravitational pressure gradient with the same *y*-intercept as the average of the 5 trees. **b**, Leaf mass:area ratio (g m^{-2}) of second-year internodes increases with height. **c**, Foliar carbon isotope composition (δ^{13}C, ‰) increases with height within the crowns of 5 trees over 110 m tall and among the tops (filled circles) of 16 trees from 85 to 113 m tall. **d**, Light-saturated photosynthetic rate per unit mass (nmol CO_2 g^{-1} s^{-1}) decreases with height. The regression line is fitted to data from six trees. Different symbol types denote different trees and are consistent for **a**–**d**.

expanded than leaves of the host tree in the same light environment, and (2) when a fallen branch from the upper crown of a tall redwood was potted in wet soil and allowed to root with the branch exposed to high light, the new leaves produced were much more expanded than the existing leaves. It is likely that in very tall trees, components of water potential, notably turgor, are important determinants of LMA and related anatomical features, just as they are along soil moisture gradients[12].

To assess further the physiological consequences of declining water potential with height, we measured stable carbon isotope composition (δ^{13}C) and leaf photosynthesis. The δ^{13}C value (‰) of plant tissues expresses the photosynthetic discrimination against $^{13}CO_2$ compared with $^{12}CO_2$ and is a common metric of long-term water stress, ranging from -20‰ to -34‰ in plants such as redwood that have the C_3 photosynthetic pathway[15]. When water stress reduces stomatal conductance, CO_2 concentration in the intercellular air spaces of leaves (C_i) declines, and this lessens the enzymatic discrimination against $^{13}CO_2$, causing δ^{13}C to increase. In redwood, foliar δ^{13}C (‰) was correlated with height (Fig. 1c, exponential fits of the form $\delta^{13}C + 31 = b_1 \exp(b_0 h)$, $b_1 = 0.681 \pm 0.434$, $b_0 = 0.033 \pm 0.005$, $0.78 \le R^2 \le 0.94$, $0.0001 \le P \le 0.002$). The highest δ^{13}C was always observed at the treetop and averaged -22.2 ± 0.6‰ at $\ge$110 m. This is the highest published foliar δ^{13}C for tall trees and is close to the apparent limit for C_3 plants[16–18]. We also found a significant relationship of δ^{13}C (‰) to height for the treetop foliage of 13 trees from 85 m to 110 m tall plus 3 trees taller than 112 m (Fig. 1c, $\delta^{13}C + 31 = 1.928 \exp(0.0131\,h)$, $R^2 = 0.321$, $P = 0.022$, $n = 16$). That δ^{13}C was higher (less negative) at the tops of trees than at the same height within tree crowns probably indicates the effect of shading in reducing foliar δ^{13}C (ref. 15). Nonetheless, patterns both within and among trees demonstrate a strong increase of δ^{13}C with height in redwood, indicative of increasing water stress.

High values of δ^{13}C occur when stomatal conductance is strongly limiting to photosynthesis, as in plants experiencing low water potentials due to soil moisture stress[15,16]. Rather than soil moisture stress, however, it is likely that in tall trees the reduction in water potential due to gravity and path length resistance causes stomatal conductance to increasingly limit photosynthesis with height[6,19]. The treetop δ^{13}C of about -22‰ corresponds to a flux-weighted C_i of ~160 p.p.m. during the assimilation of CO_2 into new biomass. This is similar to the average daily C_i estimated from our *in situ* gas exchange measurements near the tops of two 112-m-tall trees during autumn (170 ± 11 p.p.m.). Thus, integrated δ^{13}C and instantaneous gas exchange indicate that stomatal conductance is increasingly limiting to photosynthesis with height, as reported for other conifers up to 65 m tall[19,20].

Laboratory gas exchange measurements of foliage cut from different heights and re-hydrated to uniformly high water potentials enabled us to examine the consequences of height for photosynthesis in the absence of a direct influence of low water potential. Light-saturated photosynthesis per unit leaf area ($P_{\mathrm{max,a}}$) did not vary with height ($R^2 = 0.012$, $P = 0.78$), averaging 5.6 μmol CO_2 m^{-2} s^{-1}. Photosynthesis per unit leaf mass ($P_{\mathrm{max,m}}$) decreased with height (Fig. 1d, $P_{\mathrm{max,m}} = -0.455h + 55.3$, $R^2 = 0.88$, $P = 0.0002$), however, indicating a lower potential photosynthetic return on biomass invested in leaves at greater heights. The $P_{\mathrm{max,m}}$ of 110-m foliage was 28% of that at 80 m and only 16% of that at 50 m. Because light levels decline exponentially with depth in forest canopies[2], actual differences in photosynthesis per unit biomass are probably smaller than indicated by our

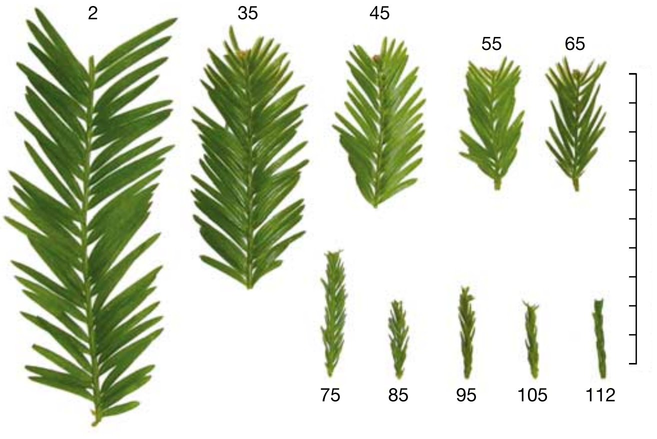

Figure 2 Variation in leaf structure with height in redwood. Leaf length and the angle between the long axis of the leaf and supporting stem segment both decrease with height. Numbers denote the sample height in m. Scale divisions are cm.

Figure 3 Leaf structure can vary independently of light environment. The upper panel shows foliage of an epiphytic redwood (expanded, light-green leaves) and adjacent foliage (unexpanded, darker-green leaves in background) of the host redwood at 95 m in the same light environment. The lower panel shows the new, more expanded foliage (at branch tips) that developed next to the existing unexpanded foliage on a detached upper crown (>90 m) branch after it was rooted in wet soil and kept in high light. Both examples support the view that variation in light environment explains little of the variation in leaf structure in redwood (see text).

measurements at light saturation. Nonetheless, photosynthetic capacity per unit foliar mass declines with height, and we hypothesize that this results from the observed changes in leaf structure. High LMA is associated with high tissue density and increased allocation of biomass to structure, including thicker cell walls[12,21]. These changes can increase internal resistance to CO_2 diffusion within leaves[22,23], reducing photosynthesis and contributing to high $\delta^{13}C$ values. We speculate that the universal influence of gravity on water potential gradients in tall trees underlies structural changes in photosynthetic tissues that, along with increased stomatal regulation, reduce photosynthesis and carbohydrate availability for height growth.

Our studies of the tallest redwoods reveal gradients in physiological and structural features that support hypotheses of height limitation due to hydraulic constraints[4,6]. Water potential, turgor, leaf structure, carbon isotope composition, and photosynthesis all change with height as they do along gradients of soil moisture stress, consistent with a general role for water availability in determining leaf functional traits[12,21]. Height gradients of these variables also allowed us to address the potential biophysical limit to height in redwood. To estimate a maximum height in the current environment barring mechanical damage, we calculated the height at which the functional variables we examined would reach a limit value (Table 1).

Low water potential affects growth severely when the formation of embolisms by cavitation reduces hydraulic conductivity[8]. Whereas it is not uncommon for shorter trees to operate at water potentials that cause considerable loss of hydraulic conductivity, cavitation avoidance may be critical for height growth in tall trees. Great height may prevent recovery of lost hydraulic function by embolism dissolution, the standard model for which requires that xylem pressures rise to within a few tenths of 0 MPa (ref. 24), higher than is possible in a water column held by tension above a few tens of metres. Our measurements of xylem vulnerability to cavitation in upper crown branches (109 m) of five trees over 110 m tall indicate that loss of hydraulic conductivity begins as xylem pressure drops to −1.9 MPa (Supplementary Information), slightly lower than the lowest pressure we recorded at the tops of the tallest trees at midday. The xylem pressure–height relationship (Fig. 1a, Table 1) estimates a pressure of −1.9 MPa at 122 m, increasing to 132 m for a limit value of −2.0 MPa. It is likely that lower water potentials and cavitation do occur in tall redwoods, mature individuals of which may experience severe droughts during life spans of up to 2,200 years (refs 25, 26). It may be during such episodes that the upper crown dies back, as evidenced by our observations that nearly all very tall redwoods have multiple tops, the original leader having died and been replaced repeatedly.

Surveys of several hundred terrestrial plant species across diverse biomes report values of LMA from 20 $g\,m^{-2}$ for thin planar leaves of herbaceous species to a maximum of 833 $g\,m^{-2}$ for the scale-like leaves in *Juniperus monosperma*, a short coniferous tree of arid regions and, like redwood, a member of the Cupressaceae[12,21]. Using 833 $g\,m^{-2}$ as the maximum possible for redwood, the LMA–height relationship (Fig. 1b, Table 1) estimates a maximum height of 122 m. If the limiting value of LMA is allowed to increase by 10%, the maximum height increases to 126 m.

For C_3 plants, the apparent limit of foliar $\delta^{13}C$ is the approximately −20‰ reported for plants of arid environments[16–18]. The overall within-crown $\delta^{13}C$–height relationship (Fig. 1c, Table 1) estimates a $\delta^{13}C$ of −20‰ at 130 m. The sensitivity of this estimate to the limiting $\delta^{13}C$ value is low; heights of 134 m and 125 m are estimated for $\delta^{13}C$ of −19‰ and −21‰, respectively.

A linear extrapolation of maximum photosynthesis versus height (Fig. 1d, Table 1) predicts that $P_{\mathrm{max,m}}$ in saturating light would decline to 0 at 125 m. Carbon import from elsewhere in the tree may support early growth of new leaves, but the trend in foliar $\delta^{13}C$ with height (Fig. 1c) indicates at most a minor quantitative significance of carbon subsidies from the lower crown.

Taken together, these height trends in ecophysiological variables indicate that the maximum height of redwood at our study site in current environmental conditions is 122 to 130 m. The reduction in water potential with height reduces leaf expansion and photosynthesis, the latter directly via increased stomatal regulation, as evidenced by $\delta^{13}C$, and indirectly by altering leaf structure (LMA), which in turn may further constrain carbon balance. Several additional lines of evidence support a limit to tree height for redwood that is taller than today's tallest trees and near the estimates from our regression analyses. First, our measurements indicate that the tallest redwoods are growing by up to 0.25 $m\,yr^{-1}$. Second, over 95% of the original old-growth redwood forest has been logged[26], and it is likely that redwoods taller than today's giants were felled[5]. Third, we analysed the height gradient in foliar $\delta^{13}C$ reported for Douglas-fir[20] ($\delta^{13}C = 0.060h - 27.5$, $R^2 = 0.999$, $P = 0.005$) and estimated by linear extrapolation that $\delta^{13}C$ would reach −20‰ at 125 m. Finally, the maximum tree height we predict for redwood and Douglas-fir is similar to the 126 m of the tallest reliably measured gymnosperm of the past, a Douglas-fir[5].

The tallest redwoods today stand in large reserves where intact forest structure sustains moist conditions and buffers trees against wind. The trees in this study, which include the first, second, fourth, sixth and eighth tallest known individuals on Earth, all occur within the largest contiguous old-growth redwood forest remaining (Humboldt Redwoods State Park, California), a reserve protecting 89 of the 116 tallest redwoods. (Measurements of redwoods throughout the species' range in California have found 116 individuals over 107 m; C. Atkins and M. Taylor, personal communication.) At reserves further north and closer to the coast, stronger storms may explain the lower heights (~100 m), yet similar relationships of water potential and $\delta^{13}C$ to height[27] as we observed in the tallest redwoods. At the drier inland margin of redwood's natural distribution in northern California, maximum tree height is lower (~80 m), yet treetop values of minimum water potential (−1.9 MPa) and maximum $\delta^{13}C$ (−22‰) are similar to those at 110 m in the tallest redwoods. Thus a similar physiological ceiling may be reached at different physical heights depending on water availability, with storm damage reducing realized heights at sites that are otherwise optimal. Tree height should also vary over time as climate fluctuates, and linking top dieback dates and growth rates to past climate may reinforce our physiological interpretation of height limitation. Climate and atmospheric change will affect the height to which redwoods grow, the outcome depending on the combined effects of elevated atmospheric CO_2 concentration and altered temperature and moisture on tree water relations and carbon balance[28]. ☐

Table 1 **Maximum height predictions for redwood, *Sequoia sempervirens***

Dependent variable	Equation	Limit value of dependent variable	Maximum height (m)
Ψ, midday (MPa)	$\Psi = -0.00973h - 0.712$	−1.9	122
LMA ($g\,m^{-2}$)	$\mathrm{LMA} = 37.43\exp(0.0255h)$	833	122
$\delta^{13}C$ (‰)	$\delta^{13}C = 0.559\exp(0.0229h) - 31$	−20	130
$P_{\mathrm{max,m}}$ ($nmol\,g^{-1}\,s^{-1}$)	$P_{\mathrm{max,m}} = -0.434h + 54.3$	0	125

The relationship of physiological and structural variables to height in redwoods at Humboldt Redwoods State Park, California. The equations describe the relationship of the dependent variable to height for data from all study trees combined. See text for explanations of limit values for dependent variables.

Methods

Tree access

We accessed tree crowns by shooting arrows trailing filament over branches with a powerful bow. Rope was then hauled over the branches and climbed via mechanical ascenders. Access to the treetop was achieved by arborist-style techniques. Heights were measured by lowering weighted fibreglass measuring tapes from the treetop to average ground level.

Physiological measurements

Water potential of small branches (≤15 cm length) located within 1 to 3 m of the main trunk was measured using a pressure chamber (PMS Instruments). Measurements of photosynthesis used a portable photosynthesis system (LI6400, LiCor) with a 2 cm × 3 cm chamber with red/blue LED light source. Photosynthesis was measured under controlled conditions: air temperature, 22 ± 1 °C; CO$_2$ concentration, 365 ± 10 p.p.m.; vapour pressure deficit, 1.2 ± 0.2 kPa; light, ≥1,400 µmol photons m^{-2} s^{-1}). Samples used for laboratory measurements of photosynthesis and pressure–volume relationships were cut from different heights, then re-cut immediately under water, allowed to re-hydrate overnight, and then measured. This produced high water potentials (−0.6 ± 0.3 MPa) and allowed comparisons of photosynthetic capacity without the influence of height-related variation in water potential. During these measurements, the C$_i$ values did not differ significantly in foliage from different heights (239 ± 16 p.p.m., $P = 0.42$). Turgor was estimated by the pressure–volume method[29].

Morphological measurements

To determine LMA, projected surface areas of 10 second-year internodes from each sample height were measured using a digital surface-area meter (Delta T Instruments). Samples were oven-dried at 70 °C, weighed, and mean LMA calculated as g m^{-2}. Area and mass measurements included the entire foliated internode.

Stable carbon isotope composition

δ^{13}C of foliage samples was analysed at the Colorado Plateau Stable Isotope Laboratory (http://www4.nau.edu/cpsil/). In 2000, second-year internodes were collected at different heights, dried (70 °C), ground to 40 mesh, and then a subsample was pulverized, encapsulated in tin, and combusted (CE Instruments NC2100) at 1,000 °C. The resultant CO$_2$ was purified and its ^{13}CO$_2$/^{12}CO$_2$ ratio was analysed by isotope-ratio mass spectrometry (Delta Plus XL, ThermoQuest Finnigan) in continuous-flow mode. The δ^{13}C values were expressed as the relative abundance of ^{13}C versus ^{12}C compared with a standard (Pee Dee Belemnite): $\delta^{13}\mathrm{C} = (R_{\mathrm{sam}}/R_{\mathrm{std}} - 1)1{,}000‰$, where R_{sam} and R_{std} are the ^{13}C/^{12}C ratios in sample and standard, respectively. The standard deviation of repeated measurements of secondary standard material was <0.1‰ (external precision).

Light environment

Hemispherical photographs were taken directly above leaf sample locations throughout tree crowns using a digital camera on a self-levelling mount. Photographs were analysed with WinSCANOPY (v.2002a, Régent Instruments Inc.) to calculate direct site factor, which is the average proportion of direct radiation received during the 12-month growing season.

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Authors' contributions G.K., S. S. and G.J. conceived and conducted the experiments, and G.K. and S.S. analysed the data and co-wrote the paper. S. D. and G. K. conducted the xylem cavitation experiments.

Competing interests statement The authors declare that they have no competing financial interests.

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Perceived luminance depends on temporal context

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Brightness—the perception of an object's luminance—arises from complex and poorly understood interactions at several levels of processing[1]. It is well known that the brightness of an object depends on its spatial context[2], which can include perceptual organization[3], scene interpretation[4], three-dimensional interpretation[5], shadows[6], and other high-level percepts. Here we present a new class of illusion in which temporal relations with spatially neighbouring objects can modulate a target object's brightness. When compared with a nearby patch of constant luminance, a brief flash appears brighter with increasing onset asynchrony. Simultaneous contrast, retinal effects, masking, apparent motion and attentional effects cannot account for this illusory enhancement of brightness. This temporal context effect indicates that two parallel streams—one adapting and one non-adapting—encode brightness in the visual cortex.

We report here a novel illusion in which temporal relationships affect brightness perception. Two flashes appeared on either side of a fixation point: one was brief (56 ms), the other long (278 ms; Fig. 1a). Observers reported which flash appeared brighter. When flashes of identical luminance had simultaneous onset, subjects