Predicting the limits to tree height using statistical regressions of leaf traits

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Summary

• Leaf morphology and physiological functioning demonstrate considerable plasticity within tree crowns, with various leaf traits often exhibiting pronounced vertical gradients in very tall trees. It has been proposed that the trajectory of these gradients, as determined by regression methods, could be used in conjunction with theoretical biophysical limits to estimate the maximum height to which trees can grow.
• Here, we examined this approach using published and new experimental data from tall conifer and angiosperm species.
• We showed that height predictions were sensitive to tree-to-tree variation in the shape of the regression and to the biophysical endpoints selected. We examined the suitability of proposed end-points and their theoretical validity. We also noted that site and environment influenced height predictions considerably.
• Use of leaf mass per unit area or leaf water potential coupled with vulnerability of twigs to cavitation poses a number of difficulties for predicting tree height. Photosynthetic rate and carbon isotope discrimination show more promise, but in the second case, the complex relationship between light, water availability, photosynthetic capacity and internal conductance to CO_2 must first be characterized.

Key words: height growth, hydraulic limitations, leaf mass area, carbon isotope discrimination, tree crowns.

Introduction

The limits to height growth in trees have been studied with considerable intensity in recent years, with an 'hydraulic limitation' hypothesis (HLH; Ryan & Yoder, 1997) shaping much of the work. The HLH states that as trees get taller and hydraulic pathways get longer, water supply to the uppermost foliage becomes increasingly restricted by gravity and friction. These restrictions require increasing stomatal closure to maintain leaf water balance, but this inhibits gas exchange to the point that a positive carbon balance cannot be achieved. This hypothesis has generated considerable controversy (Becker *et al.*, 2000; Bond & Ryan, 2000; Mencuccini & Magnani, 2000), with an increasing awareness that compensatory mechanisms modify the predictions of the original hypothesis

(McDowell *et al.*, 2002; Barnard & Ryan, 2003; Zaehle, 2005; for a review see Ryan *et al.*, 2006). Compensations for increased resistance to water flow resulting from a longer hydraulic path can include changes to leaf area: sapwood area ratios (Becker *et al.*, 2000) or tapering of xylem conduits within the pathway (West *et al.*, 1999; Anfodillo *et al.*, 2006), which tends to render total resistance independent of pathlength. Of course, hydraulic limitations owing to resistance are only operative during transpirational flow, whereas limitations owing to gravity are present continuously. Compensatory mechanisms to eliminate the effects of gravity on the water column do not exist and hence this force must be countered at the leaf level via osmotic adjustment, a process that comes with a metabolic cost.

Despite compensatory mechanisms to aid water supply to the leaves of tall trees, some impediment to water supply in

very tall species seems unavoidable and a recent study by Koch *et al.* (2004) presented evidence strongly in favor of the HLH to explain height growth limitations in the world's tallest tree species *Sequoia sempervirens*. These authors studied multiple traits that exhibit vertical gradients within tree canopies and used regressions to identify a common point of convergence which might represent the limits to tree height. A key concept was that traits are plastic only within a range set by biophysical limits. If traits change deterministically with tree height, growth beyond certain heights will be biophysically impossible. Moreover, if the causal link between 'height' (or its biophysically relevant cofactor such as gravity) and a given trait can be identified, and the same factor is involved for a suite of traits, then a single limiting factor has been identified. Using this approach, Koch *et al.* (2004) identified water potential (and its effect on cell turgor and leaf function) as the key factor limiting height growth, in agreement with the hydraulic limitation hypothesis.

In evaluating this new approach, the present authors are aware of data sets both in the literature and of our own, which suggested that considerable modification may be required to apply it to other species and sites (the latter also alluded to by Koch *et al.*, 2004).

Our aim in this paper is to take our own data collected for a number of tall tree species, including *S. sempervirens*, as well as some data in the literature, and subject it to the same approach used by Koch *et al.* (2004). The purpose was to investigate how species or site affects height predictions using this approach and what other components might need to be added to, or removed from, the existing model in order to make it more widely applicable. To this end we examined data for three of the four key traits presented by Koch *et al.* (2004, Table 1) to predict maximum tree height, for which we had available data.

Materials and Methods

Sites in the USA

Sequoia sempervirens (D. Don) specimens were sampled from three locations in coastal California. The first site ('Big Basin') was located near the south-central part of the redwood distribution range (Big Basin State Park, CA, 37°10′ N

122°14′ W). Owing to logistical constraints, a single 65 m tree on a west-facing slope (altitude 300 m) was selected for sampling. Two further sites were located in a central region of the *S. sempervirens* distribution range (Sonoma County, CA, 38°24′ N 122°59′ W). One of these sites (Sonoma Edge) was on the exposed western edge of an old-growth forest stand abutting a vineyard and here a 60-m tall specimen was selected. This is a mature edge with trees reaching ages in excess of 700 yr old. Edge trees possess crowns with branches that extend the entire height of the tree. The third site (Sonoma Interior) was approx. 230 m due east from the Sonoma Edge. Here a 67-m tall tree was selected. All of the trees at this interior location possessed crowns with branches and foliage only in the upper half of the tree; below this light was very low because of the proximity to neighboring trees, and this presumably led to trees not supporting branches here. At all three sites, the individual trees selected were part of a larger group of trees being monitored as part of a water relations experiment (Burgess *et al.*, 2006; Dawson *et al.*, 2007), but logistics required us to focus on one specimen at each 'site'. Canopy access was by fixed climbing ropes.

Leaf mass per area (LMA)

For each of the *S. sempervirens* trees already described, a minimum of five branches (in some cases 10) approx. 5 mm in diameter were harvested from different heights within the crown of the *c.* 60-m tall *S. sempervirens* specimens. Branches were chosen to be as similar as possible in age, distance from main stem (1 m), aspect and orientation. In this way we aimed to retain vertical canopy position as the dominant variable and not confound this with absolute hydraulic pathlength. Because the lowest branches in these tall specimens were generally 20–30 m from the ground, a sixth sampling position we termed 'understory', was obtained by collecting branches from smaller adjacent specimens or burl-sprouts from the parent plant. From each branch, each leaf bearing 'branchlet' or internode was removed from the main branch and passed through a leaf area meter (LI-3100; Li-Cor, Lincoln, NE, USA). Following measurement of leaf area, leaves were dried at 70°C to a constant dry weight and then recorded. The LMA was then calculated as g m^{-2}.

Table 1 Height predictions (m) for five tall tree species based on leaf mass area (LMA) and carbon isotope (δ^{13}C) profiles and the model of Koch *et al.* (2004)

	LMA Predicted height (± SE)	δ^{13}C Predicted height (± SE)	Actual height (approx.)
Sequoia sempervirens	66 (3)	79 (5)	113 (Koch *et al.*, 2004)
Eucalyptus diversicolor	411 (33)	87 (10)	80.5 (ISAAC, 2006)
Pseudotsuga menziesii	60		126 (Koch *et al.*, 2004)
Pinus monticola	93		69 (van Pelt, 2001)
Pinus ponderosa	94		80 (van Pelt, 2001)

Data for *Pseudotsuga menziesii*, *Pinus monticola* and *Pinus ponderosa* are from Marshall & Monserud (2003a,b).

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Leaf carbon isotope analysis

An average of three samples were collected per height, per tree, over a range of different heights. Leaves were sampled at a distance approx. 1 m from the stem of each tree and oven dried at 60°C for 3 d. Each sample was bulked, subsampled and then ground in a dental mill (Wig-L-Bug; Bratt Technologies, NJ, USA) to a fine powder. Powdered sample, 4 ± 0.2 mg, was placed into a tinfoil capsule before being analysed on a PDZ Europa Scientific 20/20 isotope ratio mass spectrometer at the Center for Stable Isotope Biogeochemistry, UC Berkeley (http://ib.berkeley.edu/groups/biogeochemistry/). Carbon isotope values ($\delta^{13}C$) are expressed in delta-notation (‰) relative to the V-PDB standard. Long-term external precision for the analyses is ±0.11‰.

Xylem pressure potential/leafy twig water potential

Vertical gradients in xylem pressure potential (leafy twig water potential) were measured by dispatching two climbers to collect leafy twigs simultaneously from the top and bottom of the live crown of a single tree. Further samples were taken as one climber moved up and the other climber moved down towards the middle of the tree to avoid biasing measurement of the vertical gradient. Leafy twigs were selected as close to the main stem as possible (1 m or less) and once cut, samples were placed in a polythene or polyester bag and sent down a fixed line to the base of the tree. Two operators used two PMS-1000 pressure chambers (PMS Instruments, Corvallis, OR, USA) to measure the balancing pressure (Ritchie & Hinckley, 1975) of two to four replicates per height with a minimum delay (5–10 min) from time of cutting. Weather conditions during the August 2001 date when *S. sempervirens* was sampled at Sonoma County were overcast and humid (> 80% humidity) such that transpiration was not likely to be rapid.

Light levels

The within canopy light gradient for the Sonoma Edge tree was measured during overcast conditions by pulling a pyrano-meter (LI200X; Li-Cor) and datalogger (CR10X; Campbell Scientific, Logan, UT, USA) through the canopy along a rope and measuring at regular intervals.

Australian sites

Karri, *Eucalyptus diversicolor* L. forms forests up to 80–90 m tall in the highest rainfall (approx. 1200 mm) areas of south-western Australia. The umbrella-shaped canopies of *Eucalyptus diversicolor* present considerable access challenges using fixed rope techniques. However, a number of large specimens in south-western Australia have previously served as fire lookout towers. To this end, steel climbing pegs were driven into the

main stem and platforms extending above the reach of the main stem were also constructed. These provisions permit ready access to foliage throughout the crown, including the uppermost leaves. Three pegged trees, the Bicentennial tree, Gloucester tree and Diamond tree all grow within a few kilometers of each other in the Pemberton-Manjimup region of south-western Australia (approx. 34 °S 116 °E).

Methods for LMA and $\delta^{13}C$ were as for US sites except that samples from heights within *c.* 1 m of each other were pooled to provide an average of five samples per height, per tree. Methods for xylem pressure potential/leafy twig water potential and light levels were identical to those for US sites. Weather conditions during the January 2004 date when *E. diversicolor* was sampled were partly cloudy and moderately humid (> 53%).
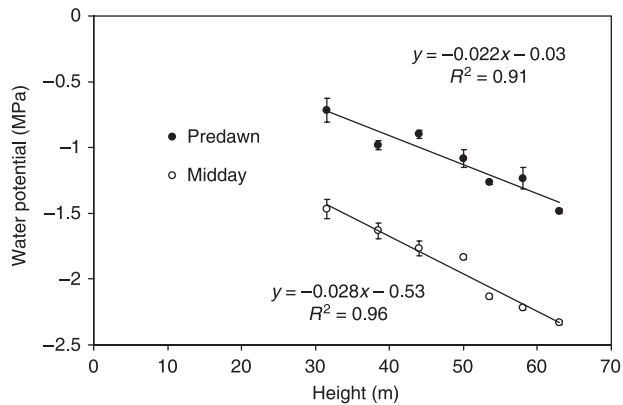
Results

Xylem pressure potential/leafy twig water potential

Figure 1 shows the vertical gradient in leafy twig water potential in a single large *S. sempervirens* ('Sonoma Edge') tree during summer (August). While we measured gradients in three trees over several different seasons, we present these data from one of the tallest of the three trees during the driest summer conditions to represent the steepest gradients and lowest absolute leafy twig water potentials measured for this species at our sites.

Figure 2 shows the vertical gradient in leafy twig water potential in a single large *E. diversicolor* tree during summer. Again, although we measured two trees over four seasons, these data from the tallest tree during summer represent the steepest gradients and lowest absolute leafy twig water potentials yet measured for this species.
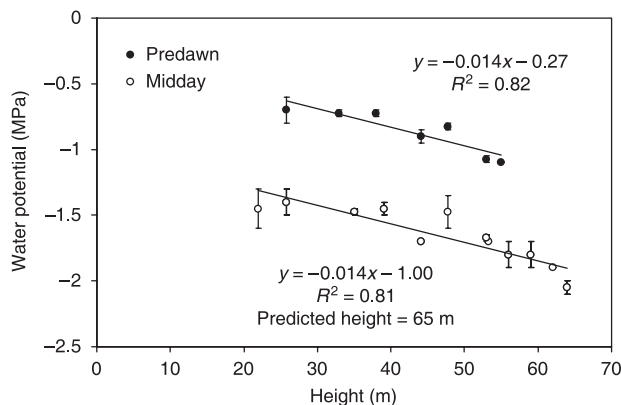
Fig. 1 Vertical gradient in leafy twig water potential in a single large *Sequoia sempervirens* tree at Sonoma County, CA, USA, during summer (August, 2001). Height predictions based on the model of Koch *et al.* (2004) are also shown. Closed circles, pre-dawn; open circles, midday.

Fig. 2 Vertical gradient in leafy twig water potential in a single large *Eucalyptus diversicolor* tree during summer (January, 2004). Height predictions based on the model of Koch *et al.* (2004) are not shown because of insufficient information on vulnerability to cavitation. Closed circles, pre-dawn; open circles, midday.

Leaf mass per unit area

**Data from *S. sempervirens* at Big Basin and Sonoma sites** Figure 3 shows a statistically significant ($F = 659.41$, d.f. = 1, $P < 0.000$), exponential increase in LMA with branch height. A statistically significant (SYSTAT version 10.0, SSI, San Jose, CA, USA; ANCOVA $P < 0.05$) difference in LMA was also evident among trees ($F = 12.225$, d.f. = 2, $P = 0.001$) although the shape of the relationship was not significantly different ($F = 1.606$, d.f. = 2, $P = 0.230$). Because of differences in LMA among trees we did not pool the data as in the case of Koch *et al.* (2004). Instead, we subjected all three height trends from each individual tree to the model of Koch *et al.* (2004). Using the theoretical maximum LMA value suggested by Koch *et al.* (2004) of 833 g m^{-2}, which is for the scale-like

leaves of the arid-zone conifer *Juniperus monosperma*, these relationships predicted maximum heights of 61 for the Sonoma Exterior tree, 67 for the Sonoma interior tree and 71 m for the Big Basin tree (see Table 1).
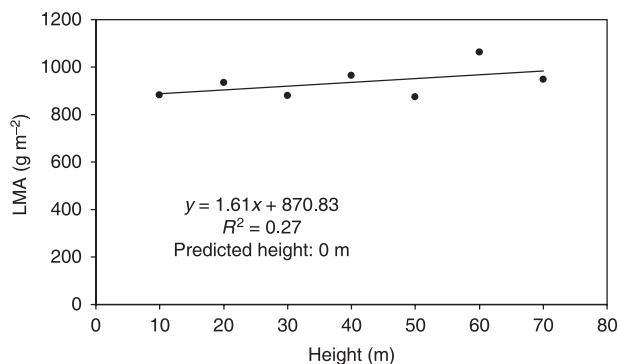
Data from other tall conifer species Marshall & Monserud (2003a,b) measured vertical gradients in specific leaf area (SLA, the inverse of LMA) in western white pine (*Pinus monticola*), ponderosa pine (*Pinus ponderosa*) and interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) in northern Idaho. We used the inverse of Marshall & Monserud's (2003a,b) SLA equations to calculate heights where LMA would reach the theoretical maximum height predicted by Koch *et al.* (2004). The approximate heights are 60 m for interior Douglas-fir, 93 m for western white pine and 94 m for ponderosa pine, compared with actual recorded maximum heights of 69 m, 91.5 m and 69 m, respectively (van Pelt, 2001, see Table 1).

Limited data collected at Calaveras, CA, for a single *Sequoiadendron giganteum* specimen showed a linear increase in LMA with height, but all values were above the theoretical maximum suggested by Koch *et al.* (2004), thus yielding a null height prediction (Fig. 4) compared with recorded heights of 67–83+ m for the largest specimens found today (van Pelt, 2001).
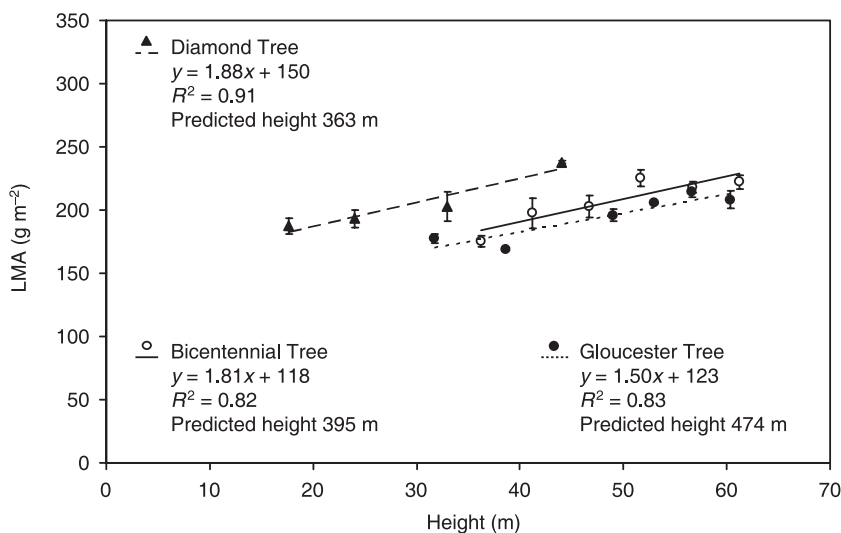
Data from tall angiosperms As for *S. sempervirens*, Koch *et al.*'s (2004) model was applied to LMA data for each individual *E. diversicolor* tree, rather than for pooled data. A linear fit was used to describe the trends in each case (Fig. 5). Heights where LMA would reach Koch *et al.*'s (2004) theoretical maximum value ranged from 363 to 474 m. This contrasts dramatically with, and clearly overestimates, maximum recorded heights of approx. 80 m (see Table 1).
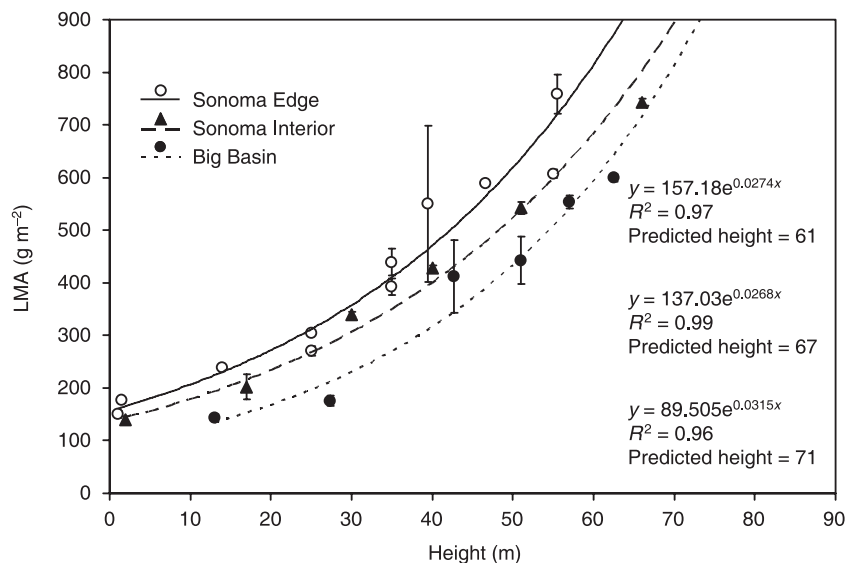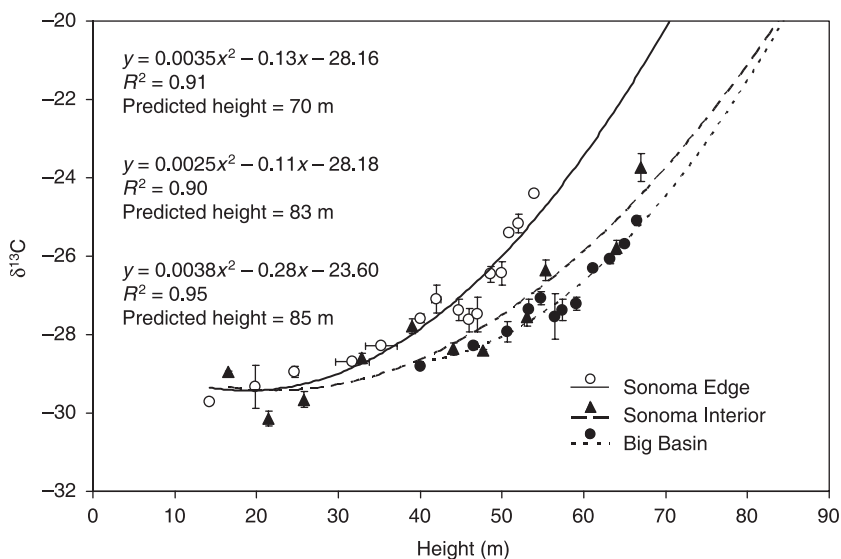

Fig. 3 Vertical gradients in leaf mass area (LMA) with height for three sites/individual *Sequoia sempervirens* trees in north central California, USA. Height predictions based on the model of Koch *et al.* (2004) are also shown. Open circles/solid line, Sonoma Edge; triangles/dashed line, Sonoma Interior; closed circles/dotted line, Big Basin.

$y = 157.18e^{0.0274x}$
$R^2 = 0.97$
Predicted height = 61

$y = 137.03e^{0.0268x}$
$R^2 = 0.99$
Predicted height = 67

$y = 89.505e^{0.0315x}$
$R^2 = 0.96$
Predicted height = 71

Fig. 4 Vertical gradient in leaf mass area (LMA) with height for *Sequoiadendron giganteum* growing at Calaveras, CA, USA. Height predictions based on the model of Koch *et al*. (2004) are also shown.

Leaf carbon isotope composition

Figure 6 shows a statistically significant increase ($P < 0.05$) in leaf carbon isotope ratio with tree height for all *S. sempervirens* trees. As shown, there was an approximately 6‰ change over the range of heights we measured. The shape of the relationship between carbon isotope discrimination and height did not differ significantly among trees/sites (using polynomial regression; $P > 0.05$).

Figure 7 shows a statistically significant increase ($P < 0.05$) in leaf carbon isotope ratio with tree height for all *E. diversicolor* trees/sites, with approximately a 4‰ change expressed over the height range we measured. As with the polynomial relationship between carbon isotope discrimination and height in *S. sempervirens* (Koch *et al*., 2004 and Fig. 6) a polynomial fit best described the trends in each case.

Fig. 5 Vertical gradients in leaf mass area (LMA) for three *Eucalyptus diversicolor* trees growing in the Manjimup/Pemberton region of southern Western Australia. Height predictions based on the model of Koch *et al*. (2004) are also shown. Diamond/dashed line, Diamond tree; open circles/solid line, Bicentennial tree; closed circles/dotted line, Gloucester tree.


Fig. 6 Vertical gradients in carbon isotope discrimination ($\delta^{13}C$) with height for three sites/individual *Sequoia sempervirens* trees in north central California, USA. Height predictions based on the model of Koch *et al*. (2004) are also shown. Open circles/solid line, Sonoma Edge; triangles/dashed line, Sonoma Interior; closed circles/dotted line, Big Basin.

Fig. 7 Vertical gradients in carbon isotope discrimination ($\delta^{13}C$) for three *Eucalyptus diversicolor* trees growing in the Manjimup/Pemberton region of southern Western Australia. Height predictions based on the model of Koch *et al.* (2004) are also shown. Diamond/dashed line, Diamond tree; open circles/solid line, Bicentennial tree; closed circles/dotted line, Gloucester tree.
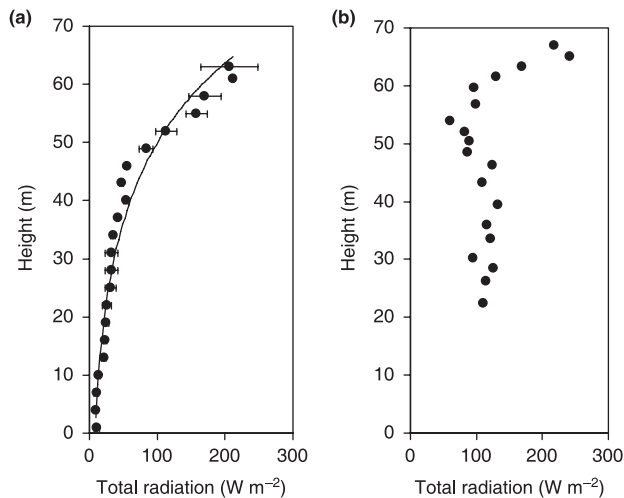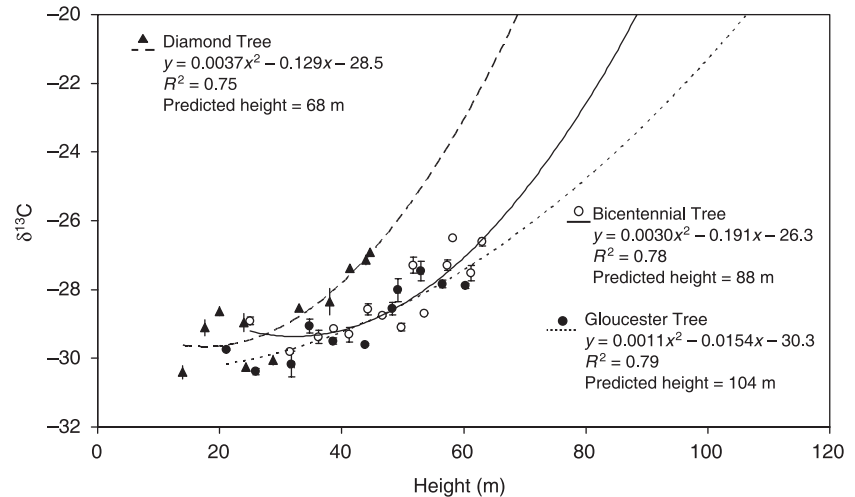
Fig. 8 Light environment for (a) 'Sonoma Edge' *Sequoia sempervirens* tree growing at Sonoma County, CA, USA, and (b) 'Bicentennial tree' *Eucalyptus diversicolor* growing at Pemberton, Western Australia, during overcast conditions (April 2002 and June 2004, respectively).

Light levels

Figure 8 shows the light environment of a *S. sempervirens* crown (A, 'Sonoma Edge') and an *E. diversicolor* crown (B, 'Bicentennial Tree'). The light environment of 'Sonoma Edge' was likely brighter than 'Sonoma Interior' or 'Big Basin' because of its edge position. Also, *E. diversicolor* forests are typically more open than *S. sempervirens* forests.

Discussion

Xylem pressure potential and embolism

The first parameter used in the model of Koch *et al.* (2004) to gauge height limitations in *S. sempervirens* was xylem pressure

potential (XPP). The argument of Koch *et al.* (2004) is that, if leafy twig water potentials (presumed to approximate XPP) at the top of trees decrease to a level where cavitation begins, leaf water supply will be permanently impaired because of the difficulty of cavitation repair under tension in conifers. The lowest leafy twig water potential we have ever measured for *S. sempervirens* at our drier southern sites is -2.05 MPa (Fig. 1) but, in general, our values agree well those reported by Koch *et al.* (2004) for their sites (i.e. no lower than -1.9 MPa) except that in our case such values occurred at lower heights (65 m). Our vulnerability curve data (Burgess *et al.*, 2006) also broadly agree with those of Koch *et al.* (2004), but suggest *c*. 2% embolism at typical midday water potentials. Whether 0%, 2% or another value is worth differentiating among by further sampling hinges on the central question of whether any embolism repair under tension in tall conifers possible, and under what time-frame (i.e. do cavitation events outstrip repair leading to accumulating xylem dysfunction)? Koch *et al.* (2004) pointed out that the most reliable information at the time (for *Laurus nobilis*) suggested that XPP must rise above -0.3 MPa before any embolism reversal occurs (Hacke & Sperry, 2003). Owing to the static water potential gradient in xylem resulting from gravity (termed gravity potential gradient, or GPG by Koch *et al.*, 2004), such small tensions are extremely unlikely at the top of tall trees, although we previously raised the possibility that water supply directly through leaves of *S. sempervirens*, as occurs during rain and fog (Burgess & Dawson, 2004) might reduce xylem tensions sufficiently to aid embolism reversal (Tognetti *et al.*, 1999). More recently, however, there are reports of embolism repair at greater tensions (e.g. -1 MPa, Domec *et al.*, 2006) which provide more scope for the possibility of repair in tall trees. A second possibility is that a supply of new xylem tissues the following season may reduce the need to repair embolized conduits.

The case of *E. diversicolor* is quite different from that of *S. sempervirens*. Our preliminary data suggest a PLC_{50} of

approx. 1–1.5 MPa for *E. diversicolor* (mid-crown twigs) in agreement with values published for the closely related *E. globulus* of 1.02–1.2 MPa (Pita *et al.*, 2003). The water potential data presented in Fig. 2, which were collected during summer for the tallest specimen we could access, represent a kind of 'worst case scenario' for cavitation. Taken with our estimates of PLC_{50}, water potential data suggest considerable embolism would routinely be present in *E. diversicolor*. A target of 0% embolism is thus neither realistic nor apparently necessary: the conclusion that repair at height is possible in this tall species seems unavoidable. This view is encouraged by evidence for repair under tension in other angiosperms (Bucci *et al.*, 2003; Domec *et al.*, 2006) and see (Konrad & Roth-Nebelsick, 2005). If 0% embolism is not a suitable limit value for height growth in this species, then perhaps the concept of runaway or catastrophic cavitation could be used (Tyree & Sperry, 1988). Once a certain level of water stress begins to cavitate and embolize some vessels, the remaining vessels must transport water faster to meet evaporative demand, increasing tensions in these vessels and leading to further embolism. This can result in a rapidly escalating cycle of cavitation (Tyree & Sperry, 1988; Nardini & Salleo, 2000). The requisite conditions of initial water stress, sustained demand for water and insufficient periods of time for embolism repair may be reached quite rapidly under critical environmental conditions (e.g. hot conditions for just a few to many hours or days in a row). These conditions may vary with season and soil water status. Thus, to use runaway cavitation instead of 0% cavitation as a parameter for determining height growth, we may need to monitor environmental conditions and plant water status for numerous seasons and in trees of different height in order to elucidate threshold conditions beyond which recovery does not occur. This will include not only an evaluation of vulnerability curves, but information on the duration and frequency of critical weather conditions. We believe this sort of information will be valuable to understanding long-term patterns of top dieback (Rice *et al.*, 2004).

Should another role for XPP also be emphasized?

Given the uniform minimum XPP values for *S. sempervirens* measured by Koch *et al.* (2004) across different sites (−1.9 MPa), and the fact that our measurements at much more southerly sites were in agreement, the idea that this reflects a 'physiological ceiling' is appealing, although obviously the height of this 'ceiling' is different for drier sites. However, we believe follow-up studies should also test whether XPP thresholds are more immediately linked to leaf-level mechanisms such as regulation of cell turgor and stomatal aperture, as a possible alternative to branch xylem cavitation. A major role for low turgor pressure limiting height growth in tall trees by reduced cell expansion and slowed carbon sink has been proposed by Ryan *et al.* (2006).

Leaf mass area

The second parameter used in the model of Koch *et al.* (2004) to gauge height limitations in *S. sempervirens* was leaf mass area. Here Koch *et al.*'s (2004) idea is that decreases in cell turgor pressure caused largely by gravity impede leaf expansion. Poor leaf expansion limits light capture and gas exchange capabilities (see also the conclusions of Woodruff *et al.*, 2004), such that architectures which yield LMA values above 833 g m^{-2} are not found among a wide surveys of plants (i.e. indicating a biophysical limit?). Using this approach, our data suggested maximum heights for *S. sempervirens* range from *c.* 61–71 m. Our crude surveys suggest that this is indeed the approximate maximum height for *S. sempervirens* at our sites, although at least some trees exceed 80 m (A. Ambrose, pers. comm.). Our findings can be reconciled with Koch *et al.*'s (2004) model if we remember their caution that their predictions of maximum heights for *S. sempervirens* of 122–130 m were for '(their) study site in current environmental conditions'. Clearly, if our more southerly sites are subject to water limitations that add to the limitations caused by gravity, then Koch *et al.*'s (2004) model would predict trees to reach biophysical limits sooner.

Although the above interpretation seems straightforward, we hesitate to adopt it without further confirmation because of the lack of correspondence with data for other species. *Sequoiadendron giganteum*, which is closely related to *S. sempervirens* showed a completely different LMA profile (more linear than exponential) and yielded LMA values above the maximum suggested by Koch *et al.* (2004), thus not permitting a positive value for maximum height to be calculated. The value of 833 g m^{-2} may need revising upwards in this case. However, we would point out that our data are based on leaves that have not been peeled from the thin strand of xylem tissue which supports them. Approximately half the length of the scale-like leaves of this species covers the stem material such that it is hard to distinguish leaf from stem structure: removing the leaves inflates their projected surface area and retaining them inflates the weight of the leaves by the presence of xylem tissue. Our values may thus be an overestimate of LMA for this species. Despite questions over the exact magnitude of LMA values for *S. giganteum*, it is interesting to note that while *S. giganteum* and *S. sempervirens* are close relatives, LMA profiles are quite different in shape and magnitude. This raises interesting questions as to the role of their different habitat vs genetics, light environment, etc. While three recent studies (Marshall & Monserud, 2003a,b; Koch *et al.*, 2004; Woodruff *et al.*, 2004) emphasize the role of GPG in determining LMA, other studies have emphasized the role of light (Ellsworth & Reich, 1993; Bond *et al.*, 1999; Han *et al.*, 2003; Niinemets *et al.*, 2004) or exposure (which combines factors such as temperature, wind speed and humidity (Sack *et al.*, 2006)). The most parsimonious reconciliation of these studies is simply that multiple factors play a role in determining

LMA. In support of the role of light and exposure we note the much more open stand and crown structure of *S. giganteum* compared to *S. sempervirens* that may lead to less steep gradients in LMA.

The results for LMA profiles in *E. diversicolor* were similar to those of *S. giganteum* in that they were linear, but produced unrealistic height predictions (363–474 m, nearly 300–400 m taller than ever corroborated in nature). It could be argued that we have chosen an inappropriate endpoint for a broadleaf angiosperm: choosing one of the highest values found in broad-leaved species (732 g m^{-2} for the shrub *Hakea corymbosa*; Wright *et al.*, 2004) yields height predictions ranging from 310 to 406 m; restricting the value to the highest found among tree species (485 g m^{-2} for *Capparis linearis*; Wright *et al.*, 2004) yields heights of 178–242 m. In all cases the predicted heights are much too great. In this case, deciding which value represents biophysical limit is difficult, particularly since not all angiosperms are broad-leafed and needle-leaved species such as *Hakea recurva* ssp. *recurva* can have LMA values of 1510 g m^{-2} (Wright *et al.*, 2004). Certainly the genetic constraints that dictate basic leaf architecture need to be considered in determining biophysical limitations.

In considering hydraulic limitation as a determinant of LMA, it is instructive to compare the results for *E. diversicolor* with those of *Eucalyptus* species that grow under much more water-stressed conditions. *Eucalyptus salmonophloia*, for example, reaches water potentials of below −5 MPa but grows to nearly 30 m while only having an LMA of approx. 300 g m^{-2} (P. Mitchell, unpublished). This serves as a reminder that many species can maintain turgor under much lower water potentials than those found at the tops of very tall tree species. Thus, while limits to LMA might have biophysical underpinnings, and LMA is affected by turgor, biophysical limits to turgor maintenance are clearly not being reached in the tall species investigated here.

The above considerations lead us to believe that LMA *per se* is not useful for predicting biophysical limits to tree height. Nevertheless, species-specific LMA profiles may provide useful information on how site characteristics such as water availability and light environment affect tree growth.

Leaf carbon isotope composition

The third parameter used in the model of Koch *et al.* (2004) to gauge height limitations in *S. sempervirens* was leaf carbon isotope composition, $\delta^{13}C$. The shapes of the vertical trends we measured for *S. sempervirens* at a more southerly location in its distribution differed from those of Koch *et al.* (2004) in that the best fit was a polynomial rather than exponential function. Our trends predicted heights of 70–85 m, similar to those recorded at our site (above). As for the case with LMA, these shorter heights are in keeping with Koch *et al.* (2004) caveats concerning of site and environment conditions. We also note that a lesser height was predicted for the 'Sonoma

Edge' tree, which, by virtue of its position at the edge of the stand has both a more uniform vertical light environment (Fig. 8a) and is likely often subjected to greater water stress.

For *E. diversicolor*, polynomial regressions of carbon isotope ratios produced height predictions of 68–104 m, which are not dissimilar from actual heights recorded for this species. The critical $\delta^{13}C$ value of −20‰ selected by Koch *et al.* (2004) for conifers appears appropriate for *E. diversicolor*, given that Pate & Arthur (1998) found maximum $\delta^{13}C$ values of phloem sap in very stressed *E. globulus* specimens to be −20.2‰. These authors reported that if values reached minus −19‰, the trees would die soon after. The major difficulty with our data appears to be the large range in predicted heights produced by considerable tree-to-tree variation.

Tree-to-tree variation argues against a universal constraining factor such as the GPG being the determinant of carbon isotope composition and reminds us that there is more than one factor which influences carbon isotope ratios of foliage. Carbon isotope composition reflects a balance between supply and demand for CO_2 at the site of carboxylation within the leaf (Farquhar *et al.*, 1989). On the supply side, leaf water status and hence stomatal conductance (g_s) or aperture are important determinants of the amounts of $^{13}CO_2$ and $^{12}CO_2$ that become incorporated into the leaf organic matter. As g_s or stomatal aperture declines with greater leaf water stress (lower water potentials), the supply of CO_2 also declines leading to an overall decline in discrimination against $^{13}CO_2$. This may be further exacerbated by leaf thickness and changes in mesophyll conductance of CO_2 to the sites of assimilation as recently discussed by Warren and Adams (2006). On the demand side, light level as well as the actual rates of carbon assimilation are important determinants of leaf $\delta^{13}C$ (Dawson *et al.*, 2002) because of how they each impact the incorporation of $^{13}CO_2$ and $^{12}CO_2$ into leaf sugars. If demand is high and leaf internal CO_2 concentrations low then the degree of discrimination against $^{13}CO_2$ declines. This would occur at higher light levels in the upper tree crowns and if leaf N and Rubisco concentrations are increased this would lead to enhanced assimilation (Farquhar *et al.*, 1989). We would argue that the steeper $\delta^{13}C$ (and LMA) trends in *E. diversicolor* and for *S. sempervirens* (note particularly the forest edge site, 'Sonoma Edge') than those reported by Koch *et al.* (2004) are at least in part a reflection of the greater and more uniform light levels, particularly in the lower canopy (see Fig. 8a,b) of these relatively open sites, compared with relatively closed redwood forests, which have an exceptionally high leaf area index (Westman & Whittaker, 1975) measured by Koch *et al.* (2004).

A recent study by Duursma & Marshall (2006) supports our view that hydraulic constraints are not the main determinant of within-crown variation in leaf $\delta^{13}C$. They found that shorter, open grown trees had a steeper gradient in leaf $\delta^{13}C$ than did larger, mature trees. Here, the gradient in photosynthetic demand seems more important than the gradient in water availability. In keeping with this idea, Duursma &

Marshall (2006) found that leaf $\delta^{13}C$ correlated most strongly with leaf N concentration. It would seem that interpreting the supply demand balance reflected by carbon isotope ratios is incomplete without evaluating the economics of photosynthesis within the leaf against the economics of the leaf water budget. Since the isotope ratios and water potentials exhibited by these tall trees species are not extreme values for the plant kingdom, we should perhaps be looking for a break-even point in the economics of osmotic adjustment and turgor maintenance, leaf architecture and gas transport, and photosynthetic yield.

The final and perhaps most important parameter used in the model of Koch *et al.* (2004) to gauge height limitations in *S. sempervirens* was photosynthesis per unit leaf mass, which we were unable to address within the scope of this critique. There is considerable and sometimes conflicting information on how this parameter relates to the question of limits to tree height (McDowell *et al.*, 2002; Barnard & Ryan, 2003). Further, a recent model proposed by Buckley & Roberts (2006) suggests that low *g* and *A*, but high leaf area at the tree top may maximize crown photosynthesis. Clearly, further research is needed to address these questions. In our view the work of Koch *et al.* (2004) has made some of the most promising measurements to date in this regard. We would urge an expansion of these types of measurements to include leaf N concentrations (Duursma & Marshall, 2006) and leaf thickness (Hanba *et al.*, 1999; Warren & Adams, 2006) which can impact photosynthesis.

Conclusions

By comparing data from different sites and species for three of the four parameters used by Koch *et al.* (2004) to predict maximum tree height, we have raised a number of questions for further research into the limits to tree height growth.

Xylem pressure potential: First, in order to be confident in setting the critical value for xylem pressure potential for conifers as that which permits 0% embolism, we believe we need to exclude experimentally the possibility of embolism repair in tall conifers. If some repair is possible, then the threshold may need to be adjusted downwards. Where repair is likely, then an alternative threshold based on runaway cavitation might be preferable.

LMA: We do not believe that LMA profiles should be used to predict the limits to tree height, owing to poor results of this method with other species. Within *S. sempervirens*, LMA profiles differ between sites and thus appear to provide useful information about actual tree height at a given site; for example, shorter trees at drier sites have truncated LMA profiles. We suggest that the high foliar plasticity exhibited by *S. sempervirens* produces a LMA profile that is unique among tall species.

$\delta^{13}C$: Leaf carbon isotope composition holds promise as a predictor of maximum tree height. However, since height pre-

dictions are sensitive to the shape of the regression used, and light can influence the shape of the regression even among individual trees, it is essential to better separate light from hydraulic effects when considering vertical gradients in $\delta^{13}C$. Moreover, leaf carbon isotope discrimination can be impacted by leaf morphology and anatomy (thickness and hence the resistance to CO_2 uptake) that is correlated to changes in LMA (Duursma & Marshall, 2006). As discussed above, we believe that revisiting the simple derivation of $\delta^{13}C$ in terms of the CO_2 concentrations at the actual sites where $^{13}CO_2$ and $^{12}CO_2$ are incorporated (at the chloroplasts; Warren & Adams, 2006 and references therein) instead of just inside of the leaf in the intercellular air spaces as it is traditionally done merits further research. Such an investigation will help resolve the importance of changes in LMA on the interplay between supply, demand and internal transfer of CO_2 and its ultimate impact on leaf $\delta^{13}C$. Finally, comparisons of $\delta^{13}C$ at the tops of trees of different heights (i.e. with tops similarly illuminated), helps to separate the effects of light vs hydraulic sufficiency; this approach to measurement should be encouraged (see Koch *et al.*, 2004) and indeed experiments are already underway (A. Ambrose, unpublished).

In summary, of the four parameters used by Koch *et al.* (2004) to predict limits to tree height, our view is that LMA should be applied only when the threshold LMA can be better matched to the plants being worked on (e.g. for gymnosperms and angiosperms, broadleaf and needle-leaf), XPP thresholds must be informed by knowledge of the *in situ* levels of embolism and if embolism repair occurs (Melcher *et al.*, 2001; Bucci *et al.*, 2003; Domec *et al.*, 2006), and most emphasis be placed on N concentration, leaf carbon isotope composition and photosynthetic rate. In the case of the last two parameters, further experimental investigation of the interplay between light and water effects will be useful in interpreting the shape of vertical gradients and thus in making accurate extrapolations toward maximum tree height.

One final observation on the various shapes of regressions that might be used to predict limits to tree height: theoretically, one might expect trees to reach height limitations via biophysical limits in an asymptotic fashion. The relationships we measured did not tend towards this, implying either that the trees we measured have not approached their biophysical limits, or that the traits studied were not limiting factors. If asymptotic functions are involved, denser sampling of upper foliage will be critical in developing the right shaped curve: without this predictions are likely to have very poor sensitivity.

Ultimately, given the short life-span of research projects relative to that of the largest trees, we believe the quest to understand what governs the size of trees must also include a modeling exercise: here the effects of leaf architecture on light capture and gas diffusion, the dynamics of whole-plant water transport pathways, disturbance regimes, mechanical issues and competition algorithms all have an opportunity to be tested for the role they play, and have played over the ages, in

New
Phytologist

determining the stature of the trees we observe today. We may learn that, rather than a single universal factor constraining tree height, there may be a complex of dynamically competing rules and probabilities which etch their mark on the skyline of our arboreal world.

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New
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