

# Determinants of maximum tree height in *Eucalyptus* species along a rainfall gradient in Victoria, Australia

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**Abstract.** We present a conceptual model linking dry-mass allocational allometry, hydraulic limitation, and vertical stratification of environmental conditions to patterns in vertical tree growth and tree height. Maximum tree height should increase with relative moisture supply and both should drive variation in apparent stomatal limitation. Carbon isotope discrimination ( $\Delta$ ) should *not* vary with maximum tree height across a moisture gradient when only hydraulic limitation or allocational allometry limit height, but increase with moisture when both hydraulic limitation *and* allocational allometry limit maximum tree height. We quantified tree height and  $\Delta$  along a gradient in annual precipitation from 300 to 1600 mm from mallee to temperate rain forest in southeastern Australia; *Eucalyptus* on this gradient span almost the entire range of tree heights found in angiosperms worldwide. Maximum tree height showed a strong, nearly proportional relationship to the ratio of precipitation to pan evaporation.  $\Delta$  increased with  $\ln P/E_p$ , suggesting that both hydraulic limitation and allocational allometry set maximum tree height. Coordinated shifts in several plant traits should result in different species having an advantage in vertical growth rate at different points along a rainfall gradient, and in maximum tree height increasing with relative moisture supply, photosynthetic rate, nutrient supply, and xylem diameter.

**Key words:** adaptive crossover;  $\delta^{13}C$ ; *Eucalyptus regnans*; maximum tree height; soil fertility; substrate rejuvenation.

## INTRODUCTION AND CONCEPTUAL FRAMEWORK

Variation in maximum tree height has profound implications for the photosynthesis, growth, crown and bole dimensions, tissue allocation, hydraulic conductance, and population density of individual trees (Givnish 1995, Ryan and Yoder 1997, McDowell et al. 2011, Mencuccini et al. 2011, Larjavaara 2013), stand biomass, carbon storage, and productivity (Feldpausch et al. 2012, Hui et al. 2012, Ruiz-Benito et al. 2014), leaf area index and transpiration (Roberts et al. 2001, Falster et al. 2010), net input to ground and surface waters (Bleby et al. 2012), and the availability of suitable habitat for certain animals (Wormington et al. 2002, García-Ferced et al. 2011). Over the last three decades, several models have been advanced to account for maximum tree height and its variation with environmental conditions and plant traits. Most of these depend on one of two fundamental trade-offs, involving shifts with tree height in dry-mass allocational allometry or photosynthetic hydraulic limitation, and their impact on rates of height growth, sometimes viewed in the context

of the vertical stratification of environmental conditions (Fig. 1).

### Dry-mass allocation allometry

Givnish (1984, 1995) showed that the balance of photosynthesis against the increasing proportional allocation of dry matter (and, thus, energy) to the construction of non-photosynthetic stem and root tissue with tree height, required for mechanical stability, could account for the maximum 60-m height of *Liriodendron tulipifera*, the tallest angiosperm tree in eastern North America. The positive allometry (i.e., increasing proportion) of stem construction costs with height in eastern North America trees implies that leaf allocation should drop from ~47% of all such costs in trees 1 m tall, to 24% in trees 30 m, to 17% in trees 100 m tall, and that annual allocation to unproductive organs should increase from 53% to 83% (Givnish 1995). Increased rates of photosynthesis in brighter, moister, or more fertile habitats, greater allocation to productive leaf tissue at a given height in moister or more fertile habitats, or greater permanence of support tissue should increase maximum plant height. Likewise, tree lines should be encountered in moving toward environments that are too cold, hot, dry, wet, nutrient-poor, or dark to sustain adequate rates of photosynthesis to cover the low costs of tissue construction of even short, erect forms.

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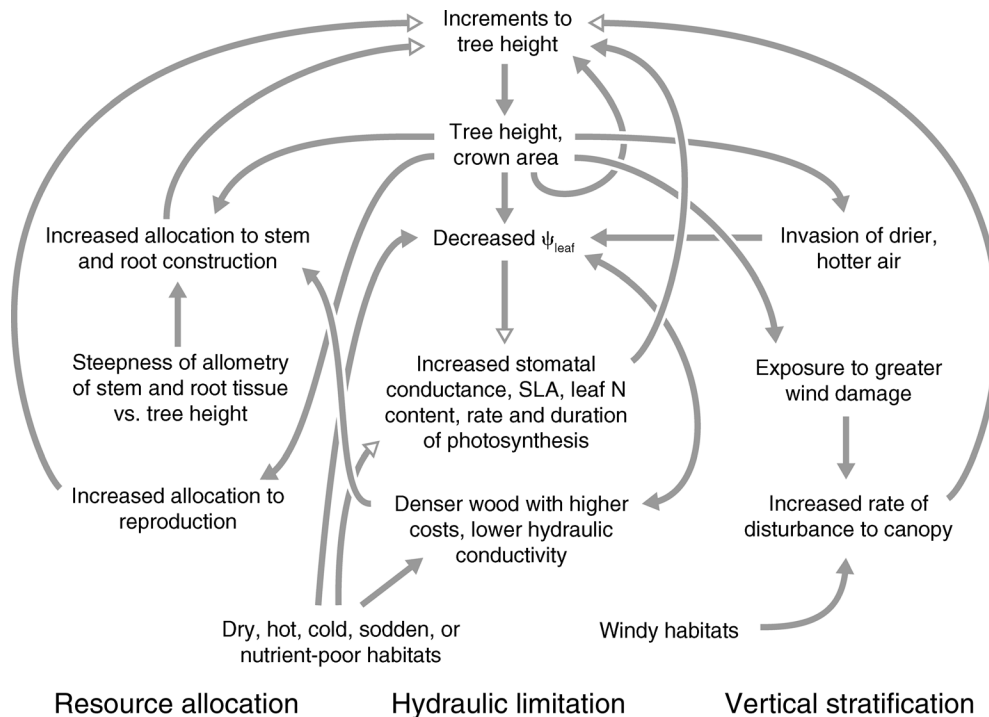


FIG. 1. Flow chart summarizing proposed positive feedbacks (solid arrowheads) and negative feedbacks (hollow arrowheads) affecting height growth, and ultimately, maximum tree height, based on trade-offs involving resource allocation, hydraulic limitation, and vertical stratification of environmental conditions. Photosynthesis and its correlates affect models based on both resource allocation and hydraulic limitation; climate and density of vegetation presumably affect the vertical stratification of conditions near the top of existing vegetation in complex ways.

Tilman (1988) argued that, if there is no allometry in dry-matter allocation to different organs with tree height, a balance of photosynthesis against catastrophic disturbance would favor greater maximum tree heights in areas with higher resource supplies or lower rates of disturbance. A balance of carbon uptake and catastrophic disturbance can indeed set maximum plant height, but the unvarying stem allocation with height in the Tilman model is counterfactual and creates what we term the "Shangri-La paradox," in which a few protected sites with, say, only 1/10 the typical rate of disturbance should produce trees 10 times as tall as seen elsewhere. Increasing proportional allocation to unproductive tissue with height should create a declining rate of height growth in taller trees, and thus a more reasonable variation in maximum height with catastrophic disturbance rate, as well as layered vegetation in which lower woody and herbaceous strata are present due to their greater shade tolerance, reflecting their lower allocation to unproductive tissues (Givnish 1995). More generally, higher rates of small-scale disturbance (e.g., occasional loss of individual leaves to herbivores, fire, or ice) should also reduce maximum tree height.

King (1990) argued that a disproportionate increase in stem *respiration* with height could set maximum tree height, but the data do not support this assumption

(Ryan and Waring 1992, Mencuccini and Grace 1996, Ryan et al. 1997, Pruyn et al. 2002). Most wood is truly dead wood, making the energy allocated to tissue construction a far better measure of stem costs than tissue respiration. Thomas (1996a) and Thomas and Bazzaz (1999) found that maximum (i.e., asymptotic) tree height in rain forest trees is positively correlated with initial rates of height growth and photosynthetic rate per unit leaf area, mass, and nitrogen content, and negatively correlated with wood density (see also King 1991), as expected on allocational grounds. Many trees commence reproduction only when they approach their maximum height (Thomas 1996b, c, 2011, Davies and Ashton 1999, Wright et al. 2005), opening the possibility that reproductive allocation and its timing help set maximum tree height, just as increased allocation to unproductive stem tissue with height can limit tree height.

King (2011) provided a meta-analysis linking the allometry of stem diameter and tissue mass to declines in the rate of height growth with increasing height, and discussed how these declines are likely to be less in crowded stands, and greater in windswept trees. As expected, tethering of wind-exposed trees reduces sway and stem allocation, resulting in higher rates of height growth (Meng et al. 2006).

### Photosynthetic hydraulic limitation

Ryan and Yoder (1997) proposed that the inevitable decline in leaf water potential ( $\psi_{\text{leaf}}$ ) with tree height, due to the increased weight of the suspended water column and greater friction along longer hydraulic pathways, could limit maximum tree height when combined with a requirement that leaf water potential be maintained above some minimum. Lower values of  $\psi_{\text{leaf}}$  in taller trees should trigger stomatal closure earlier in the day, reducing stomatal conductance ( $g$ ) and photosynthesis ( $A$ ), thereby reducing growth in biomass and height. Ryan and Yoder argued that resource-poor sites would favor shorter maximum tree heights because trees on such sites produce wood with lower permeability, resulting in critical values of  $\psi_{\text{leaf}}$  and stomatal closure at lower heights. According to their view, species with higher leaf-specific stem hydraulic conductivity ( $K_L$ ) and lower sensitivity to low values of  $\psi_{\text{leaf}}$  should be able to achieve greater heights. Absent from their argument was a recognition of how the positive allocational allometry of unproductive tissue with tree height could limit tree height, or how maximum height could be reduced on resource-poor sites by lower photosynthetic rates and increased allocation to roots.

Of 51 papers that tested assumptions of the hydraulic limitation hypothesis in the decade after it was proposed, most provided evidence consistent with that hypothesis, showing declines in midday  $\psi_{\text{leaf}}$ ,  $K_L$ ,  $g$ , and  $A$  with tree height (Ryan et al. 2006). There was, however, no evidence that reductions in stomatal conductance or photosynthesis at the leaf level with tree height were adequate to account for reductions in wood production (Barnard and Ryan 2003, Ryan et al. 2004). Koch et al. (2004) documented declines in  $\psi_{\text{leaf}}$ , turgor pressure, and  $A_{\text{mass}}$  with tree height, and increases in leaf mass per unit area (LMA) and  $\delta^{13}\text{C}$  (the relative enrichment of a sample in  $^{13}\text{C}$  relative to the V-PDB standard, which becomes less negative with increases in the relative stomatal limitation of photosynthesis in  $\text{C}_3$  plants [Farquhar et al. 1982, 1989]), within and among crowns of *Sequoia sempervirens*. Ambrose et al. (2009) provided in situ data showing that stomatal conductance does, in fact, decline toward the tops of *Sequoia* crowns.

Koch et al. (2004) extrapolated the drop in maximum net photosynthesis per unit leaf mass of rehydrated foliage with height to predict a maximum height of 125 m at which  $A_{\text{max}} = 0$  (even though  $A_{\text{area}}$  showed little change with height), close to the maximum heights based on extrapolations of shifts in  $\psi_{\text{leaf}}$  and  $\delta^{13}\text{C}$  to limits based on the supposed onset of xylem cavitation at approximately  $-2.0$  MPa and minimum values of  $\delta^{13}\text{C} = -20\%$  in arid-zone plants. This study has been criticized on several grounds (Burgess and Dawson 2007, Netting 2009; cf. Du et al. 2008, Koch and Sillett 2009); when it is parameterized for other species (e.g., *Eucalyptus diversicolor* of southwestern Australia), it grossly overestimates maximum tree height (Burgess and Dawson 2007). There are additional problems with the

Koch et al. approach. First, tissue construction costs and the increasing proportional allocation to non-photosynthetic tissue with tree height were ignored; their inclusion would place a substantially lower limit on tree height (Givnish 1984, 1995, Becker et al. 2000, King 2011). Second, measuring photosynthesis on rehydrated foliage ex situ almost surely underestimated the effect of height on gas exchange. Third, while plant species can differ in their sensitivity to water potential,  $\psi_{\text{leaf}}$  at the top of the tallest *Sequoia* is much less negative than the minimum observed in many desert plants that can survive and photosynthesize under much harsher conditions (e.g., less than  $-6.0$  MPa for *Larrea tridentata* in North American deserts [Naumberg et al. 2004], and less than  $-6.5$  to possibly  $-10$  MPa in *Acacia aneura* and *A. ayersiana* in Australian mulga [O'Grady et al. 2009, Page et al. 2011, Cleverly et al. 2013]), making it unlikely that low water potentials in tall trees per se halt carbon gain. Increases in  $\delta^{13}\text{C}$  (and, thus, decreases in the carbon isotope discrimination  $\Delta$ ) with tree height appear to be quite general, both within tree crowns and among well-illuminated crown tops, with the rate of decline being least in gymnosperms and greatest in temperate angiosperms (McDowell et al. 2011). Optimal stomatal conductance and  $\psi_{\text{leaf}}$  should decline together under a variety of models: (1) to maximize photosynthesis for a given total amount of transpiration, assuming that  $A$  does not depend on  $\psi_{\text{leaf}}$  (Cowan and Farquhar 1976, Cowan 1986), given that less water is available in the stem and the ground when predawn  $\psi_{\text{leaf}}$  is more negative; (2) to maximize photosynthesis when  $A$  does depend on  $\psi_{\text{leaf}}$ , given that optimal  $g$  should drop not with decreasing  $\psi_{\text{leaf}}$  but with increasing values of  $\partial A/\partial \psi_{\text{leaf}}$  and decreasing values of plant hydraulic conductance (Fig. 6.3–6.5 in Givnish 1986), with the latter, at least, decreasing with tree height and concomitant decreases in  $\psi_{\text{leaf}}$ ; and (3) to avoid runaway cavitation, in which stomatal closure should respond to  $\psi_{\text{leaf}}$  (Brodribb and Holbrook 2003), not  $\partial A/\partial \psi_{\text{leaf}}$ . The trend toward producing smaller, thicker leaves with lower photosynthetic capacity per unit energetic investment under water stress at the tops of trees demonstrated by Koch et al. also appears to be fairly general (Ishii 2011).

Numerous studies have documented changes in tree anatomy or morphology that compensate, though only in part, for the expected declines in  $\psi_{\text{leaf}}$ ,  $K_L$ ,  $g$ ,  $A_{\text{mass}}$ , and exposure to runaway cavitation with tree height (Becker et al. 2000, Mencuccini 2003, Zaehle 2005, Ryan et al. 2006, Addington et al. 2009, Ambrose et al. 2009, Gleason et al. 2012). Maintaining critical limitations constant with height, even if it were possible, would impose other trade-offs. In the case of  $K_L$ , for example, it would require greater allocation to sapwood and/or lower density wood (Ryan and Yoder 1997, Bucci et al. 2004), which should reduce vertical growth and competitive ability in the first case, and increase the likelihood of cavitation (Hacke et al. 2001) and reduce



PLATE 1. (Left) *Eucalyptus dumosa* in mallee near Hattah, northwest Victoria (Australia); gray mounds are clumps of spinifex grass (*Triodia*). Measurements of gas exchange using an LI-6400 photosynthesis system in progress. (Center) *Eucalyptus* woodland in central Victoria, north of Bendigo. (Right) Tall sclerophyll forest dominated by *Eucalyptus regnans* in Yarra Ranges south of Marysville, southern Victoria. Photo credits: T. J. Givnish.

tree longevity in the face of wood-eating fungi and termites in the second case (Bultman and Southwell 1976, Givnish 1995). Domec et al. (2008) found that the decline in the aperture of bordered pits of tracheids in *Pseudotsuga menziesii* with tree height, an apparently compensatory adaptation that reduces air-seeding and cavitation at very low  $\psi_{\text{leaf}}$ , also reduces conductance between tracheids, with water transport projected to drop to zero in trees 109–138 m tall, setting another limit on tree height. Xylem tapering, an increase in vessel number as vessel diameter decreases with height, can ameliorate the effects of friction-limited flow (but not gravity) on low  $\psi_{\text{leaf}}$  in tall trees (McCulloh and Sperry 2005, Petit et al. 2008, 2010).

There is substantial evidence for physiological integration at several levels within plants, with leaf photosynthetic capacity on a mass basis coupled to leaf mass per unit area and N content per unit mass (Reich et al. 1997, Wright et al. 2004a, b; but see Lloyd et al. 2013, Osnas et al. 2013), and on an area basis to stomatal conductance (Wong et al. 1979), leaf vein density (Brodribb et al. 2007, Brodribb and Feild 2010) and associated leaf hydraulic conductance (Brodribb et al. 2005), stem hydraulic conductance (Mencuccini 2003), and wood density (Bucci et al. 2004). This pattern of whole-plant integration might suggest limited latitude for compensatory change in any single trait as height varies. Yet several studies have shown that maximum tree height among species locally increases with stem hydraulic conductivity per unit leaf area (Addington et al. 2009, Zach et al. 2010, Fan et al. 2012), and therefore, often increases with xylem vessel diameter and the initial

rate of height growth and decreases with wood density (King 1991, Thomas and Bazzaz 1999, Zach et al. 2010, Fan et al. 2012, Gleason et al. 2012).

Kempes et al. (2011) present a flow-based model to account for variation in maximum tree height across the contiguous United States, supposedly also taking stem allometry into account. The absence of critical statistics (e.g., values of  $r^2$  and  $P$ ) and detailed descriptions of sub-models, however, make their claim hard to evaluate. It is also unclear whether their  $Q_0$ , the minimum water flow supposedly needed to sustain metabolism, represents an actual minimum flow or is simply a tunable parameter.

#### *Vertical stratification of environmental conditions*

Height-specific shifts in physical conditions may also constrain maximum tree height. Desiccation and ice-blasting by winds may, for example, increase leaf mortality above the boundary layer or winter snow in tundra, favoring shorter plants in more exposed microsites, as well as aerodynamically smooth canopies that force air around rather than through them. Increased vapor pressure deficit (VPD) above canopies (Hinckley et al. 2011) should depress  $\psi_{\text{leaf}}$  in twigs that project above the canopy; together with steep increases in direct solar heating and transpiration with height above the canopy due to high solar flux, such increases could strongly depress  $\psi_{\text{leaf}}$ , reduce stomatal conductance and photosynthesis, favor denser wood with finer xylem elements and lower hydraulic conductance (Hacke et al. 2001), and thereby limit further height growth.

### Synthesis

The potential effects of these mechanisms on maximum tree height, incorporating the effects of allocational allometry, hydraulic limitation of photosynthesis, and vertical stratification of environmental conditions, are summarized in Fig. 1. The integration of these disparate effects has not been advocated in explicit terms previously. The complexity of the interactions implied by this graphical model make it difficult to predict, at least in quantitative terms, how tree height and its potential determinants should vary along real environmental gradients. Here we propose that if maximum tree height along a moisture-supply gradient is set by hydraulic limitation *alone*, with little or no shift in mesophyll photosynthetic capacity due to other shifts in the environment, carbon isotope discrimination  $\Delta$ —an inverse measure of relative stomatal limitation of photosynthesis (Farquhar et al. 1989)—should not vary along that gradient; all trees at their maximum height should show the same degree of stomatal limitation. Tree height should increase until  $\psi_{\text{leaf}}$  and stomatal conductance decrease to the point that net photosynthesis equals zero (Ryan and Yoder 1997, Koch et al. 2004). Alternatively, if maximum tree height along such a gradient is set by the scaling of allocational allometry *alone*, we would also expect  $\Delta$  not to vary with position on such gradients. However, if maximum tree height is set by *both* hydraulic limitation and resource allocation, we would expect  $\Delta$  to increase with moisture supply at maximum tree height, reflecting a lower degree of stomatal limitation, and thus, often a higher rate of photosynthesis, on moister sites balanced against the greater proportional allocation to unproductive stem tissue in taller trees (Givnish 1984, 1995). That is, we expect stomatal limitation to increase (i.e.,  $\Delta$  to decrease) toward drier sites with shorter trees, rather than toward taller trees on rainier sites (Fig. 2). Greater height may also reflect, in part, the lower proportional allocation of energy to root construction and respiration expected on moist, well-drained sites (Givnish 1995), and greater photosynthetic capacity of thinner leaves with higher N concentration per unit leaf mass adapted to greater stomatal conductance on such sites (Cunningham et al. 1999, Farquhar et al. 2002). A positive correlation of soil fertility or xylem vessel diameter with moisture supply would strengthen such trends. Vertical stratification of environmental conditions should affect maximum tree height only through effects on hydraulic limitation or resource allocation, and should thus not affect predictions regarding  $\Delta$ .

Although our model focuses on maximum tree height, we assume that trees maximize their rate of height growth at each height under a given set of conditions to compete successfully. Buckley and Roberts (2006) found a limit to tree height using a model that maximized carbon gain, but that limit was not maximum tree height, because “suboptimal” trees could grow indefi-

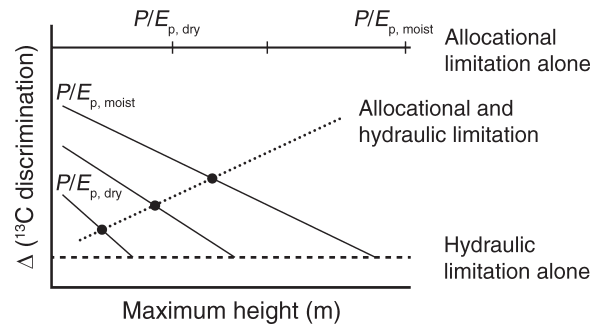


FIG. 2. Expected trends in maximum tree height and  $\Delta$  under different assumptions with shifts in relative moisture supply, as measured by the ratio of precipitation to pan evaporation. Top solid line: If maximum tree height is set by allocational limitation alone, height should increase with  $P/E_p$  while  $\Delta$  remains unchanged and at maximal value. Bottom dashed line: If maximum tree height is set by hydraulic limitation alone, height should increase with  $P/E_p$  while  $\Delta$  remains unchanged and at minimum value consistent with nearly zero growth. Diagonal dotted line: If maximum tree height is set by both allocational and hydraulic limitation, both height and  $\Delta$  should increase with  $P/E_p$ ; trees at higher values of  $P/E_p$  should achieve higher rates of photosynthesis and be less hydraulically limited to balance the greater allocational costs of height increments at greater heights. Diagonal solid lines indicate the expected relationship of  $\Delta$  to height at different values of  $P/E_p$ ; moister conditions should permit short trees to maintain higher  $\Delta$ , and for  $\Delta$  to decline less rapidly with height as a consequence of selection for lighter wood with greater hydraulic conductivity. Were the allocational cost of an increment to tree height to fall to zero in the limit, the diagonal dotted line relating  $\Delta$  to height should become shallower in slope, approaching the dashed line set by hydraulic limitation alone. Note that, at a given relative moisture supply, maximum height set by both allocational and hydraulic limitations is less than or equal to those set by one or the other limitation alone.

nately taller. In general, maximizing carbon gain vs. height growth can favor different strategies (Montague and Givnish 1996). Others have suggested that water supply per se may limit height growth, especially through the effect of reduced turgor pressure on cell division and expansion (Marshall and Monserud 2003, Woodruff and Meinzer 2011), but ignore the fact that treetop conditions are sufficiently favorable at least part of the year to permit leaf development and expansion. The related claim that carbon balance cannot set maximum tree height because nonstructural carbohydrates are not more depleted in taller trees (e.g., Sala and Hoch 2009) is not compelling in our view, because, irrespective of height, all trees must maintain reserves with which to reproduce and replace losses to herbivores and disturbances.

Here we test our model by examining how tree height and apparent stomatal limitation of photosynthesis vary with climatic conditions in *Eucalyptus* species native to a steep gradient from 300 to 1600 mm of annual rainfall in Victoria, Australia (Fig. 3). Our study transect runs from tall sclerophyll forest and temperate rain forest in the Yarra Ranges northeast of Melbourne, including some of the tallest angiosperms

in the world (~90 m), to mallee only a few meters tall near Mildura. The upper canopy of these forests is composed almost entirely of members of the genus *Eucalyptus*. In aggregate, *Eucalyptus* spans nearly the entire range of maximum tree heights seen within angiosperms, and extant species along the Victoria transect cover almost all heights seen in *Eucalyptus*, so that the Victoria transect may serve as a microcosm of worldwide variation in tree height (see Plate 1). We predict that tree height should increase with relative moisture supply, reflecting the effects of both hydraulic limitation and resource allocation; that stomatal limitation should decrease with increasing rainfall at maximum tree height; and thus that moisture supply should have a stronger effect than tree height on apparent stomatal limitation. Recent global meta-analyses show a roughly 4% increase in  $\Delta$  with rainfall from 300 to 1600 mm (Diefendorf et al. 2010, Kohn 2010), but roughly the same decrease in  $\Delta$  with tree height from 3 to 90 m across a wide range of different habitats (McDowell et al. 2011), so that the null expectation might in some sense be zero change in  $\Delta$  along the Victoria gradient.

## METHODS

### Site location

Variation in stomatal limitation with increasing rainfall has been investigated previously along rainfall gradients from the Australian periphery to the dry interior in the northern, eastern, and southwestern portions of the continent (Stewart et al. 1995, Schulze et al. 1998, Miller et al. 2001, Schulze et al. 2006, Turner et al. 2008, Hutley et al. 2011). Our Victoria transect in southeastern Australia (Fig. 3) includes a narrow, 3° band of latitude where rainfall is nearly aseasonal, total rainfall and tree height decline steeply to the north, while pan evaporation ( $E_p$ ) rises sharply and mean annual temperature and day length increase only modestly. Pan evaporation, the empirically determined rate of water loss per unit area from water in open pans, is *not* the same as potential evapotranspiration (PET), the modeled rate of water loss from short, well-watered crops, often estimated using the Penman-Monteith equation. PET varies from 0.35 to 0.85  $E_p$ , depending on external conditions (Allen et al. 1998). Soils become more alkaline and coarse-grained to the north, and elevations exceed 300 m above sea level only in the Yarra Ranges and its foothills in the south (Victorian Resources Online 2012).

Nineteen sites were chosen for study, based on (1) dominance of the canopy by native *Eucalyptus* species; (2) location on well-drained slopes or convex landforms, to avoid trees tapping shallow water tables on extensive flats; (3) greater tree height than other nearby stands; and (4) stratification of sites across the transect based on annual rainfall. The tallest trees were standing dead in the Wallaby Creek catchment of Kinglake National Park, killed by the Black Saturday bushfires of February

2010, including the skeleton of what had been until recently the tallest living tree on the Australian mainland, *Eucalyptus regnans* at 92 m (Mifsud 2002). All other stands sampled were composed entirely of living trees. Sites were chosen without detailed knowledge of past fires, but criterion (3) should have resulted in selecting sites with fewer catastrophic fires limiting tree height than others nearby. In general, fire frequency might be expected to increase from temperate rain forests and tall sclerophyll forests at high rainfall to woodlands at intermediate rainfall, and then decline with further decreases in rainfall toward mallee, given its low coverage and low rates of fuel accumulation. Natural vegetation is essentially continuous in the Yarra Ranges but becomes increasingly fragmented northward, where most naturally regenerating stands are restricted to state and national forests and parks.

### Data collection and analysis

Site latitude and longitude were measured using a hand-held GPS (GPSMap 62s, Garmin, Olathe, Kansas, USA). We used these coordinates and altitude derived from a digital elevation model to predict average annual rainfall  $P$ , pan evaporation  $E_p$ , and the ratio  $P/E_p$  using ESOCIM (Centre for Resource and Environmental Studies 2012). At each site, we estimated the heights of the tallest 3–6 individuals using a laser level (TruPulse 200, Laser Technology, Centennial, Colorado, USA). Circumferences of these individuals were taped and converted to diameters, and a reduced major-axis power-law regression of stem diameter against height was calculated. We compared this against a similar regression obtained by Niklas et al. (2006) for 420 champion trees for individual gymnosperm and dicot tree species in North America and Great Britain, and another we derived using data for the five tallest, mostly coniferous trees in each of 74 old-growth stands in southwestern Oregon kindly provided by Dr. David W. Hann of Oregon State University. Dominant *Eucalyptus* species were identified following Nicolle (2006).

To estimate tissue carbon isotope discrimination, we sampled stem wood near the base of the tree rather than leaf tissue in order to reduce the noise in discrimination values due to the relatively short lifetime of individual leaves vs. the main bole, to spatial and temporal variation in conditions facing leaves in different parts of the canopy, and to the pooling of photosynthate over potentially small parts of the canopy for the construction of individual leaves. The mixing of signals in the  $\delta^{13}\text{C}$  of wood presumably results in some attenuation of extremes in  $\delta^{13}\text{C}$  fixation throughout the canopy. Discrimination values for *Eucalyptus* did, in fact, show substantially less variation about a trend along a climatic gradient in northern Australia in wood vs. leaf tissue (Miller et al. 2001). Wood samples excluding bark from three trees were therefore collected at each site, using a battery drill to collect shavings from the outer 5

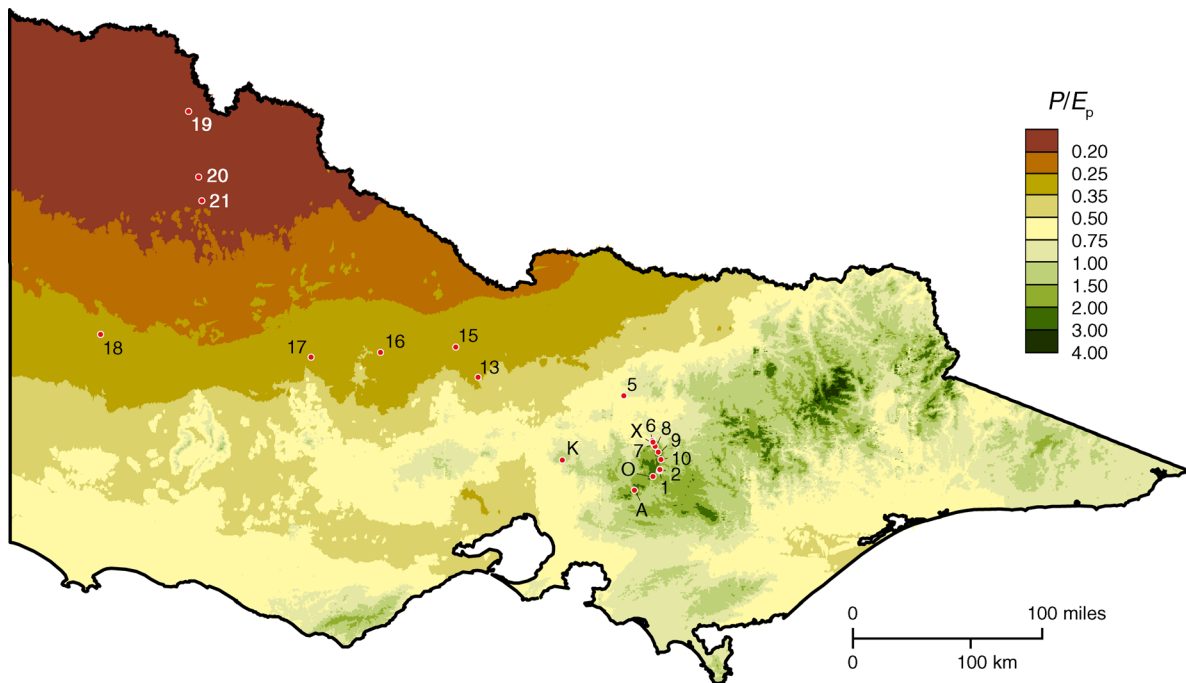


FIG. 3. Map showing the distribution of study sites along the Victoria transect in relation to the average value of the ratio of annual rainfall to annual pan evaporation ( $P/E_p$ ).

cm of the trunk at 1 m height. Shavings from the three trees were pooled and dried immediately over silica gel.

At sites outside the Yarra Ranges, fully exposed leaves reachable from the ground were collected for tissue analysis; within the Yarra Ranges, leaves torn from the upper canopy by a recent windstorm were gleaned. Leaf tissue was cut into known areas, dried over silica gel and then at 80°C, and weighed to calculate specific leaf area (SLA,  $\text{g}/\text{cm}^2$ ). Leaf N concentration per unit leaf mass ( $N_{\text{mass}}$ , mg N/g leaf) was quantified using an elemental analyzer (CE Instruments, Milan, Italy). We estimated maximum photosynthetic rate per unit leaf mass ( $A_{\text{mass}}$ ,  $\text{nmol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$ ) from SLA and  $N_{\text{mass}}$  using the equation

$$\log_{10}A_{\text{mass}} = -0.66 + 0.844 \log_{10}N_{\text{mass}} + 0.782 \log_{10}\text{SLA} \quad (1)$$

derived from an analysis of data for 269 species by Reich et al. (1998).

Twenty 1-cm cores from the upper 10 cm of soil were collected at each site, pooled, dried, and analyzed for percentage sand, silt, and clay, and percentage organic C. Concentrations of soluble  $\text{NO}_3$ , Ca, Mg, and K were determined using flame spectrophotometry; available P was measured using the Olsen technique.

Wood shavings were dried to constant mass at 80°C and finely ground. Sample  $^{13}\text{C}/^{12}\text{C}$  was measured using an Isochrom continuous-flow mass spectrometer (Micromass, Manchester, UK), following combustion in a CE Instruments elemental analyzer (noted before Eq. 1). We converted  $^{13}\text{C}/^{12}\text{C}$  ratios to discrimination values by

assuming that air has a  $^{13}\text{C}$  composition of  $-0.0078 = -7.8\text{‰}$  relative to V-PDB (Farquhar et al. 1989). Carbon isotope discrimination is negatively related to  $\delta^{13}\text{C}$

$$\Delta = (\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}})/(1 + \delta^{13}\text{C}_{\text{plant}}) \quad (2)$$

and is conveniently scaled by multiplying by 1000‰.  $\Delta$  is also roughly an inverse measure of stomatal limitation to photosynthesis. A drop in stomatal conductance  $g$  without a change in photosynthetic rate  $A$  should depress  $c_i$ , the concentration of  $\text{CO}_2$  inside the leaf's intercellular air spaces

$$c_i = c_a - A/g \quad (3)$$

where  $c_a$  is the concentration of  $\text{CO}_2$  in the open atmosphere (Farquhar et al. 1989). As a consequence of drops in  $c_i$ , carbon isotope discrimination should also decrease (Hubick et al. 1986), although strictly  $\Delta$  more nearly reflects  $c_c/c_a$ , where  $c_c$  is  $[\text{CO}_2]$  at the sites of carboxylation. Nevertheless, the gradient  $c_a - c_i$  is usually about double that of  $c_i - c_c$ , so that small values of  $\Delta$  typically reflect small values of  $c_i$ , which translate into high levels of stomatal limitation. Put another way,  $\Delta$  largely reflects  $c_i/c_a$  and so negatively reflects the ratio of photosynthesis to stomatal conductance at the time of carbon uptake (Eq. 3). Internal or external factors that increase  $A$  without greatly increasing  $g$ , or decrease  $g$  without greatly decreasing  $A$ , will tend to decrease  $c_i$  and thus  $\Delta$ .

We calculated simple regressions relating maximum tree height and  $\Delta$  to each other and annual rainfall, pan

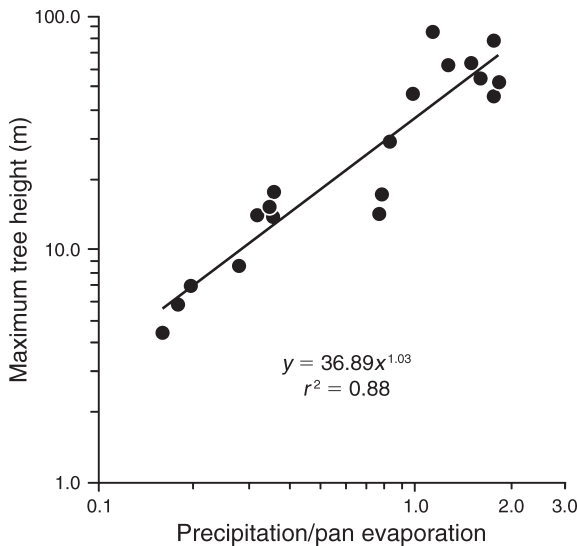


FIG. 4. Maximum tree height vs.  $P/E_p$ ; the solid line indicates least mean squares regression based on log-transformed data ( $y = 36.89x^{1.03}$ ,  $r^2 = 0.88$ ,  $P < 0.0001$  for two-tailed  $t$  test with 17 df). Both axes are logarithmically transformed.

evaporation, the ratio of rainfall to evaporation, SLA,  $N_{\text{mass}}$ , estimated  $A_{\text{mass}}$ , and various soil measures (percentage sand, silt, and clay; percentage organic C; concentrations of P, nitrate, and major cations [Ca + Mg + K]), based on nominal and log-transformed data, using Excel 14.1.0 and StatPlus 5.8.3.8.

We used simple and multiple regression to test whether  $\Delta$  decreases with N content per unit area ( $N_{\text{mass}}/\text{SLA}$ ) and increases with SLA, as observed in *Eucalyptus* from southwestern Australia (Turner et al. 2008) and a variety of  $C_3$  plants from the northeast China moisture transect (Prentice et al. 2010). We conducted a multiple regression relating  $\Delta$  to maximum height and  $P/E_p$  to determine the relative strengths of the relationships of  $\Delta$  to these factors when both are considered, and whether one or both factors had a significant effect on  $\Delta$ . We used a similar approach to evaluate the relative effect of maximum tree height ( $H$ ) and  $P/E_p$  on SLA,  $N_{\text{mass}}$ , and estimated  $A_{\text{mass}}$ . Finally, we used backward-elimination and forward-addition multiple regression models to assess the potential effect on  $\ln H$  of all environmental variables that had showed a significant univariate relationship to  $H$  (i.e.,  $\ln P/E_p$ ,  $\Delta$ , percentage sand, percentage silt, percentage organic C, P, and nitrate). We used the same procedure to evaluate potential determinants of  $\Delta$ , including  $H$  among candidate predictors. Too many missing values precluded inclusion of SLA,  $N_{\text{mass}}$ , and  $A_{\text{mass}}$  in these analyses.

## RESULTS

Estimated annual precipitation  $P$  varied from 297 to 1587 mm across the 19 sites of the 450-km Victoria transect, with the lowest rainfall near Hattah in the

mallee region in the north and the highest near Cumberland in the Yarra Ranges in the south. Modeled pan evaporation  $E_p$  ranged from 1864 to 859 mm along that same gradient. As a result,  $P/E_p$  increased more than 11-fold, from 0.16 near Hattah to 1.83 near Cumberland (Appendix: Tables A1 and A2). Elevations varied from 50 to 200 m above sea level on the northern two-thirds of the transect, and from 350 to 1000 m in the Strathbogies, Kinglake, and Yarra Ranges.

Maximum tree height showed a remarkably strong, positive, nearly proportional relationship to  $P/E_p$  when both variables were log-transformed (Fig. 4,  $y = 36.89x^{1.03}$ ,  $r^2 = 0.88$ ,  $P < 0.0001$  for 17 df, two-tailed  $t$  test). The strong correlation of  $P$  and  $E_p$  with each other produced almost identically tight fits of  $\ln$  height to  $E_p$ ,  $\ln P$ , and  $\ln E_p$ . Mean maximum tree height increased from 4.4 m in mallee near Hattah to 87.2 m at the recently burnt site at Wallaby Creek. Diameter at breast height scaled more or less proportionally to tree height across the Victorian transect ( $y = 0.026x^{0.992}$ ,  $r^2 = 0.90$ ,  $P < 0.0001$  for 17 df), in contrast with the  $\sim 3/2$  power law observed in North American champion trees and Oregon old-growth conifers (Fig. 5).

Values of  $\Delta$  increased sharply along this climatic gradient, from 14.6‰ near Hattah to 21.1‰ in the Yarra Ranges (Fig. 6A,  $\Delta = 1.81 \ln P/E_p + 19.72$ ,  $r^2 = 0.63$ ,  $P < 0.0001$  for 17 df). As predicted,  $\Delta$  showed a significant increase with maximum tree height  $H$  (Fig. 6B,  $\Delta = 1.45 \ln H + 14.31$ ,  $r^2 = 0.49$ ,  $P < 0.001$  for 17 df). Values of  $\Delta$  predicted from the regression increased by roughly 4‰ over the gradient, from  $\sim 17$ ‰ in the mallee to  $\sim 21$ ‰ in the Yarra Ranges. Regressing  $\Delta$  (‰)

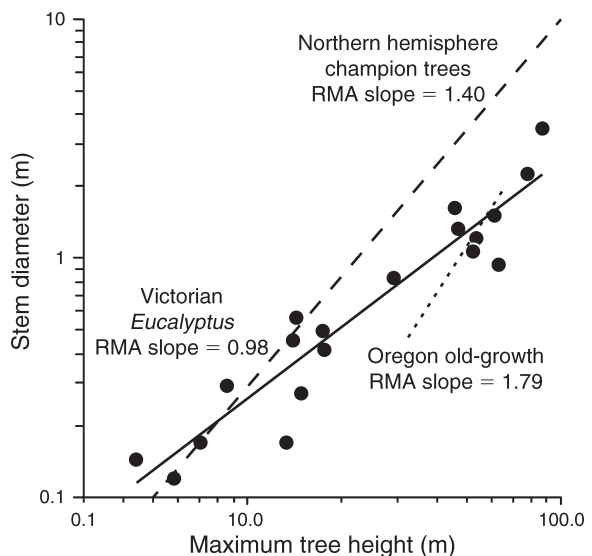


FIG. 5. Average stem diameter vs. maximum tree height; the solid line indicates reduced major axis regression based on log-transformed data ( $y = 0.026x^{0.99}$ ,  $r^2 = 0.90$ ,  $P < 0.0001$  for 17 df). The dashed line represents a similar power-law regression for 576 champion trees from North America (McMahon and Bonner 1983). Both axes are logarithmically transformed.



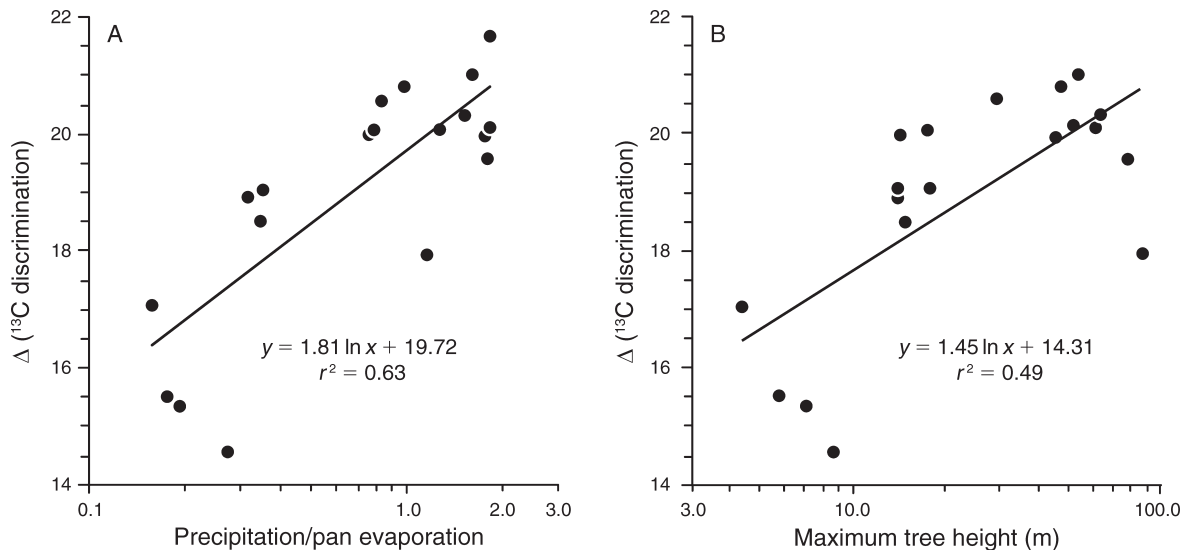


FIG. 6. Carbon isotope discrimination ( $\Delta$ ) as a function of the ratio of precipitation to pan evaporation ( $P/E_p$ ) and maximum tree height on the Victoria transect. (A)  $\Delta$  vs.  $P/E_p$  ( $\Delta = 1.81 \ln P/E_p + 19.72$ ,  $r^2 = 0.63$ ,  $P < 0.0001$  for 17 df); (B)  $\Delta$  vs.  $H$  ( $\Delta = 1.45 \ln H + 14.31$ ,  $r^2 = 0.49$ ,  $P < 0.001$  for 17 df). The x-axes are logarithmically transformed.

on log-transformed  $P/E_p$  and  $H$  resulted in a highly significant model

$$\Delta = 21.07 + 2.149 \ln P/E_p - 0.349 \ln H \quad (4)$$

( $r^2 = 0.60$ ,  $P < 0.0007$  for 16 df). Note that a given proportional change in the climatic variable  $P/E_p$  had an effect on  $\Delta$  that is 5.4 times that of a similar change in tree height; the latter varied 19.8-fold along our gradient, while  $P/E_p$  varied 11.5-fold. The multiple regression thus retrieved the expected partial increase in  $\Delta$  with  $P/E_p$  and the expected partial decrease with  $H$ , despite the significant increase in  $\Delta$  with  $H$  in the univariate regression (Fig. 6B). That is, stomatal limitation appeared to decrease toward moister conditions and increased with tree height. The overall effect of  $P/E_p$  on  $\Delta$  was nearly 4.5 times greater than that of  $H$  across the gradient, resulting in a net increase in  $\Delta$  in moving toward moister conditions and taller trees. Interpretation of this model is clouded, however, because neither  $P/E_p$  nor  $H$  had a significant effect on  $\Delta$  ( $P = 0.052$  for  $\ln P/E_p$ ,  $P = 0.68$  for  $\ln H$ ), even though their joint effect was highly significant, and even though both had highly significant effects when considered separately in simple regressions.

SLA increased significantly with  $\ln P/E_p$  and with maximum tree height (Fig. 7A, B). Leaf nitrogen concentration showed a weaker increase with  $\ln P/E_p$ , but no significant relationship to maximum tree height (Fig. 7C, D). Of the leaf parameters,  $A_{\text{mass}}$  showed the strongest increase with both  $P/E_p$  (Fig. 7E,  $y = 127.3 \cdot (P/E_p)^{0.367}$ ,  $r^2 = 0.66$ ,  $P < 0.0003$  for 13 df) and maximum tree height (Fig. 7F,  $y = 40.7 \cdot H^{0.304}$ ,  $r^2 = 0.59$ ,  $P < 0.0004$  for 13 df). Maximum photosynthetic rates on a mass basis thus increased significantly with both relative

moisture supply and maximum tree height. However, this is likely to have been driven by changes in SLA, as there were no significant changes in  $A_{\text{area}}$  with  $H$  or  $P/E_p$ . Multiple regressions preserved the positive effects of  $\ln P/E_p$  and  $\ln H$  on  $\Delta$ , SLA,  $N_{\text{mass}}$ , and  $A_{\text{mass}}$  in seven of eight cases, though the individual effects of  $\ln P/E_p$  and  $\ln H$  were not significant in any case. The effect of  $\ln H$  on  $N_{\text{mass}}$  became negative in the multiple regression on  $\ln H$  and  $\ln P/E_p$ , but the outcome essentially pointed to  $N_{\text{mass}}$  being independent of  $\ln H$ , given that the slope on the latter was  $< 10\%$  of the slope on  $\ln P/E_p$ . We found no significant relationship of  $\Delta$  to SLA or  $N_{\text{mass}}/SLA$  using simple or multiple regressions. Leaf nitrogen content per unit area showed a significant decrease with both  $P/E_p$  ( $N_{\text{area}} \text{ (g/m}^2\text{)} = 6.40 - 1.83 \ln P/E_p$ ,  $r^2 = 0.30$ ,  $P < 0.035$  for 13 df) and maximum height ( $N_{\text{area}} = 13.02 - 1.79 \ln H$ ,  $r^2 = 0.35$ ,  $P < 0.021$  for 13 df).

Soil texture varied from nearly pure sand in the mallee portion of the gradient (sites 18–21 in northwestern Victoria; Fig. 3) to sandy loams, loams, and sandy clay loams in the central and southern portions of the gradient (Appendix: Fig. A1). The percentage of sand ranged from 50% to 98.7%; percentage of silt, from 1.3% to 35%; and the percentage of clay, from 0% to 22.5%. There was no significant difference in sand, silt, or clay content in and near the Yarra Ranges (sites K, A, O, 1, 2, 10, 9, 8, 7, X, 5) vs. those in central Victoria (sites 13–17). The percentage of sand decreased significantly with  $\ln P/E_p$  ( $y = -9.11 \ln x + 63.01$ ,  $r^2 = 0.34$ ,  $P < 0.008$ , 17 df) and  $\ln H$  ( $y = -8.51 \ln x + 93.42$ ,  $r^2 = 0.34$ ,  $P < 0.008$ , 17 df). The percentage of silt showed an even stronger increase with the logarithms of relative moisture supply and maximum tree height along the gradient (Appendix:

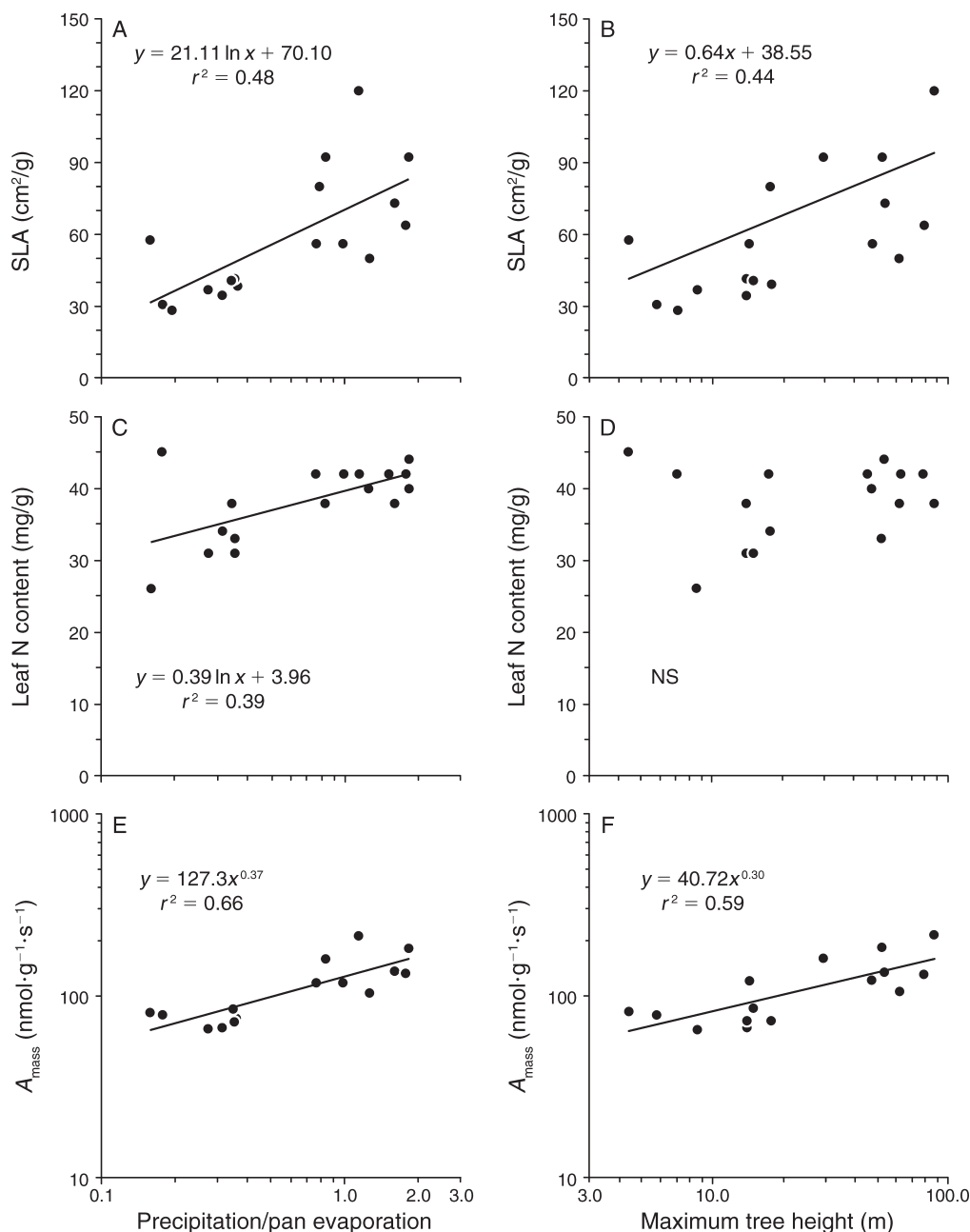


FIG. 7. (A, B) Specific leaf area (SLA) increases with  $P/E_p$  and maximum tree height.  $SLA = 21.11 \ln P/E_p + 70.10$ ,  $r^2 = 0.48$ ,  $P < 0.0025$  for 15 df;  $SLA = 0.64 \ln H + 38.55$ ,  $r^2 = 0.44$ ,  $P < 0.004$  for 15 df. The x-axes are logarithmically transformed. (C, D)  $N_{\text{mass}}$  (mg N/g dry leaf mass) increases significantly with  $P/E_p$  but not with maximum tree height along the Victoria transect.  $N_{\text{mass}} = 3.88 \ln P/E_p + 39.62$ ,  $r^2 = 0.39$ ,  $P < 0.008$  for 15 df;  $N_{\text{mass}} = 0.058 \ln H + 35.86$ ,  $r^2 = 0.08$ , NS). The x-axes are logarithmically transformed. (E, F) Maximum photosynthetic rate ( $A$ ) per unit leaf mass increases with relative moisture supply and maximum tree height.  $A_{\text{mass}} = 127.3 \times (P/E_p)^{0.37}$ ,  $r^2 = 0.66$ ,  $P < 0.0002$  for 13 df;  $A_{\text{mass}} = 40.72 \times (P/E_p)^{0.30}$ ,  $r^2 = 0.59$ ,  $P < 0.001$  for 13 df). Both axes are logarithmically transformed.

Fig. A2A, B). The percentage of clay increased toward moister sites and taller trees, but neither pattern was significant ( $P > 0.25$ ). The logarithm of soil organic C content increased significantly with both  $\ln P/E_p$  and  $\ln H$  (Appendix: Fig. A3A, B).

The combined concentrations of major cations ( $\text{Ca}^{++} + \text{Mg}^{++} + \text{K}^+$ , in milliequivalents per 100 grams [expressed as moles of cations ( $\text{mol}_c$ ) in the SI system]) showed no significant trend with either  $P/E_p$  or maximum tree height. However, nitrate concentration

increased in power-law and exponential fashion with these two variables, respectively (Appendix: Fig. A4A, B), while phosphate concentration increased in power-law fashion with both (Appendix: Fig. A5A, B).

Finally, both backward-elimination and forward-addition multiple regressions identified the same model for environmental determinants of maximum tree height

$$\ln H = 3.265 + 0.787 \ln P/E_p + 0.284 \ln[\text{nitrate}] \quad (5)$$

( $r^2 = 0.94$ ,  $P < 3 \times 10^{-10}$  for two-tailed  $t$  test;  $P < 1.5 \times 10^{-8}$  for  $\ln P/E_p$  and  $P < 0.0016$  for  $\ln[\text{nitrate}]$  with nitrate in units of milligrams per gram). That is, tree height increased significantly with both relative moisture supply and soil nitrate concentrations. Similarly, both backward-elimination and forward-additional multiple regressions identified the same model for environmental determinants of  $\Delta$  (%)

$$\Delta = 16.48 + 0.785 \ln P/E_p + 0.608 \% \text{ silt} \quad (6)$$

( $r^2 = 0.79$ ,  $P < 5 \times 10^{-6}$  for two-tailed  $t$  test;  $P < 0.047$  for  $\ln P/E_p$  and  $P < 0.002$  for percentage of silt. That is,  $\Delta$  increased significantly with both relative moisture supply and soil silt content, which we interpret as stomatal limitation decreasing as both variables increased.

#### DISCUSSION

Our study departs from most recent investigations of maximum tree height by asking not what conditions favor the tallest trees, but instead how shifts in plant traits and ecological conditions along environmental gradients favor corresponding shifts in maximum tree height. We believe that this approach is more likely to cast light on the underlying determinants of maximum tree height, and to clarify the extent to which observed shifts in plant traits are due to shifts in external conditions vis-à-vis tree height itself. Along the Victoria gradient, both allocational allometry and hydraulic limitation appear to constrain maximum tree height, the first finding of its kind.

Our data show a surprisingly strong tendency for the logarithm of maximum *Eucalyptus* height along the Victoria transect to increase with  $\ln P/E_p$  (Fig. 4) and its strong correlates there,  $E$ ,  $\ln P$ , and  $\ln E_p$ . The relationship of height to  $P/E_p$  is likely to prove more general than that to either  $E_p$  or  $P$  alone. Simply put, the supply of moisture relative to evaporative demand should constrain tree height more than the absolute supply of moisture alone, based on either the resource-allocation or hydraulic-limitation models. The observed increase of maximum height with both  $P/E_p$  and soil nitrate concentration (Eq. 5) is also expected under both models; higher photosynthetic rates, greater leaf area index (LAI), and/or lower allocation to roots due to higher nitrate concentrations should all favor greater maximum tree height by increasing carbon gain at any given height. The observed increases in SLA and leaf N concentration with increasing  $P/E_p$  are consistent with

optimality models (Givnish 1978, 2002) as is the decline in leaf N content per unit area with increasing  $P/E_p$  (Buckley et al. 2002).

The isometric scaling of *Eucalyptus* diameter with maximum tree height across the Victoria moisture-availability gradient (Fig. 5) is notable for three reasons. First, it violates the 3/2 power-law relating stem diameter and height expected among trees in a given area based on biomechanics (McMahon 1973) and metabolic scaling theory (West et al. 1999, Price et al. 2007). Second, shifts in the relationship between stem diameter and height are expected along environmental gradients, as recently predicted and shown by Lines et al. (2012) for increases in relative diameter under drier or colder conditions in Spain. It is thus surprising that our data provide evidence for a rather uniform relationship of stem diameter to height over a wide range of relative moisture supply, raising several questions about how such a pattern might arise. Third, our data show that, at greater tree heights, Victorian *Eucalyptus* are more slender than champion angiosperm and gymnosperm trees from North America. The greater slenderness of Victorian *Eucalyptus*, combined with the very low wood density of the tallest species, may help explain the extraordinary heights achieved by *Eucalyptus* in southeastern Australia, although the biases toward larger diameters in the champion-tree data set need further examination, and the Oregon old-growth data argue against *Eucalyptus* being especially slender. Our study is one of very few in which tree diameter–height allometry has been quantified in even summary fashion along environmental gradients (e.g., Lines et al. 2012), and calls for further modeling of the determinants and implications of ecological variation in diameter–height allometry.

The significant increase in  $\Delta$  with  $P/E_p$  and with  $H$  along the Victoria gradient (Fig. 6A, B) contradicts the idea that maximum tree height there is determined solely by allocational allometry or solely by hydraulic limitation (see *Introduction*). It instead supports our hypothesis that both constraints act jointly to help set maximum tree height, with greater heights achieved in moister and more fertile areas where there is less stomatal limitation of photosynthesis and (presumably) a lower proportional allocation to unproductive roots. Across the entire length of the gradient, the positive effect of relative moisture supply on  $\Delta$  appeared to be 4.5 times larger than the negative effect of tree height, explaining why we observed a net increase in  $\Delta$  in moving toward both moister conditions and taller trees (see Eq. 4). Globally,  $\Delta$  increases with moisture supply in many contexts (Schulze et al. 1998, Miller et al. 2001, Turner et al. 2008, Diefendorf et al. 2010, Kohn 2010, Prentice et al. 2010, Mencuccini et al. 2011) and decreases with tree height locally (Koch et al. 2004, Burgess and Dawson 2007, McDowell et al. 2011). Our data suggest that, when relative moisture supply and tree

height co-vary along a gradient, the effects of the former on maximum tree height will dominate.

Within-crown variation in leaf  $\Delta$  might make basal wood  $\Delta$  an unreliable indicator of stomatal limitation in trees of different heights. Yet Miller et al. (2001) found an excellent match (i.e., a constant offset) between  $\Delta$  values for leaf vs. basal wood samples of *Eucalyptus* species along the extensive rainfall gradient in northern Australia, including substantial variation in tree height. Even if wood  $\Delta$  were to vary along the length of a tree's bole, there would likely be a tight tie of basal wood  $\Delta$  to average wood  $\Delta$ , so that basal wood  $\Delta$  should be a good proxy for average leaf  $\Delta$  (see *Methods*).

The fact that our results support an interaction of allocational and hydraulic limitations in setting maximum tree height along the Victoria gradient is of fundamental importance, but should not, in retrospect, be that surprising. Given the demonstrated allometric increase with tree height in the energy spent constructing unproductive stem and root tissue (Givnish 1984, 1995, King 2011), it is simply impossible for hydraulic limitation, acting alone, to set maximum tree height. Plants must cover these construction costs, which are to be distinguished from the vanishingly small costs of wood respiration, and the relative size of such costs increases with tree height. When Koch et al. (2004) proposed that maximum tree height in *Sequoia* is set by the height at which leaf photosynthesis (mass basis) falls to zero due to hydraulic limitations, they created a paradox because *Sequoia* does get as tall as the putative maximum height, but the huge costs of yearly increments to leaf, stem, and root tissue had not been counted against carbon income. The observed decline in photosynthesis with height at any one time will, almost surely, be sensitive to recent weather conditions, so that the slope and intercept of carbon uptake,  $\psi_{\text{leaf}}$ , LMA (leaf mass per unit area), or  $\Delta$  may predict different maximum heights based on measurements at different times. The supposedly critical values of these parameters may also vary greatly among species and habitats. For example, the Koch et al. model for LMA applied to data from *Eucalyptus diversicolor* in southwestern Australia yields a predicted maximum height of 363–474 m, three to four times taller than any actual tree on Earth (Burgess and Dawson 2007)!

Why does maximum tree height on the Victoria transect track  $P/E_p$  much more closely than does  $\Delta$ ? Traditional views of hydraulic limitation include (1) declines in leaf area-specific hydraulic conductance with increasing tree height; (2) declines in  $\psi_{\text{leaf}}$  with tree height due to decreased whole-plant hydraulic conductance and increased gravitational potential; and (3) resulting decreases in average stomatal conductance (Ryan and Yoder 1997, Koch et al. 2004, Ryan et al. 2006, Hinckley et al. 2011, Mencuccini et al. 2011). Factors that might contribute to a tighter relationship of maximum tree height to  $P/E_p$  than expected based on hydraulic limitation (and thus  $\Delta$ ) alone might include (4)

increased allocation to leaves vs. roots or stems at a given height with increasing  $P/E_p$ , or conditions correlated with higher  $P/E_p$  (e.g., greater soil silt or nitrate content); (5) higher photosynthetic rates per unit leaf mass at higher  $P/E_p$  or under conditions correlated therewith, independent of the degree of stomatal limitation; (6) higher leaf area-specific conductance at higher  $P/E_p$  in trees of a given height, reflecting differences in wood density and xylem diameter and length (Thomas 1996b, Thomas and Bazzaz 1999, Zach et al. 2010, Fan et al. 2012, Gleason et al. 2012); (7) variation across species in the rate at which mesophyll photosynthetic capacity declines with decreasing  $\psi_{\text{leaf}}$  (Givnish 1986, Tezara et al. 2003, 2011, Lawlor and Tezara 2009); (8) variation across sites in which the rate at which evaporation from sunlit leaves increases with relative height at the top of the canopy; and (9) greater uncertainties in measuring average  $\Delta$  than average height. The preceding factors are all plausible ways in which resource allocation or modified hydraulic limitation effects could constrain tree height along the Victoria transect, in response to the increase in  $P/E_p$  toward the Yarra Ranges, the reduced heat load and cloudier conditions at higher altitudes and latitudes there, and the increasingly fine-grained, more P- and N-rich soils there (see Eq. 5).

Maximum tree height is unlikely to be under direct selection in *Eucalyptus* (or most other tree genera), given that it is achieved so late in life. Furthermore, in *Eucalyptus* there is unlikely to be any trade-off between shade tolerance vs. stature, given that all or almost all taxa are highly shade intolerant. We propose that different climatic and soil conditions favor different species that have the highest rate of height growth and/or survival as juveniles under those conditions, and that higher rates of initial growth on sites with high rainfall and fertile soils result in greater maximum tree height. Moister, more fertile conditions should favor species with higher SLA, leaf N concentration per unit mass, stomatal conductance,  $\Delta$ , leaf hydraulic conductance, and maximum photosynthetic rate per unit leaf mass, and lower percentage root allocation and wood density, with the latter leading to high values of stem hydraulic conductance. Indeed, in a recent analysis of gas-exchange and hydraulic traits in 120 dicot species along an aridity gradient in eastern Australia, Gleason et al. (2012) showed that plant height increased with xylem-specific hydraulic conductivity normalized by the ratio of total leaf area to total xylem area. The relationships observed accounted for 39% of height and conductivity differences within sites, but only 10% of the variance across sites. Explanatory value across sites might be greatly increased if several of the factors we listed were also surveyed across the *Eucalyptus* species found on the Victoria gradient. Monitoring growth and survival of species transplanted to different levels of rainfall could provide a direct test of the hypothesis that species distributions reflect adaptive crossover, in which species

with growth advantages at successive points along a gradient dominate the vegetation at those points (Givnish et al. 2004). Such an experiment might also provide compelling support for the adaptive value of several critical traits that vary among species found at different points along the gradient.

Purely allocational or purely hydraulic limitations may constrain maximum tree height on other gradients. For example, Cernusak et al. (2011) found that  $c_i$  varied hardly at all with rainfall (and thus, with tree height) in *Eucalyptus* and *Corymbia* along the Northern Australia Tropical Transect (Schulze et al. 1998), which accounts for the observed lack of variation in  $\Delta$  there. In our view, the lack of variation in  $A/g$ , and thus, in  $c_i$  and  $\Delta$ , across the NATT may reflect the fact that >80% of annual precipitation falls from December to March, with intense drought at other times of year. Consequently, conditions may be equally favorable for stomatal conductance during the rainy season along the entire transect. Yet tree height drops from 20.5 to 8.5 m over a fourfold change in median annual rainfall from Melville Island north of Darwin, to Kidman Springs (Williams et al. 1996). This shift in maximum tree height without a concomitant decrease in apparent stomatal limitation (i.e.,  $\Delta$ ) seems likely to reflect greater carbon gain in the north due to the longer rainy season there, as well as lower proportional allocation to roots, reflecting, in other words, variation in photosynthesis and resource allocation, *not* hydraulic limitation as traditionally conceived. The potential influence of interannual variation in rainfall and nearly annual fires setting back tree height on the NATT must, however, also be considered.

While this paper describes maximum tree height as a function of climate, and defines maximum height operationally, that height can only approximate the absolute maximum height achievable at different points along the Victoria transect. For example, one *Eucalyptus regnans* at Cumberland included in this survey was once thought to be the tallest remaining tree in Victoria, then lost its 92-m top in previous storms, is now ~87 m tall, and has regrown 5.5 m since 2001 (Mifsud 2002). The tallest tree at Wallaby Creek was 92 m tall before it and its entire stand died in the Black Saturday bushfires of 2010; its exceptional height was due not to exceptionally high  $P/E_p$  (see Fig. 3), but to exceptional age; the tallest trees there appear to have become established around 1700, long before most *E. regnans* in Victoria, and were spared fires that burnt in several areas in the Hume Range over the last century, including some within the same stand (Mifsud 2002). Just before the fires, *E. regnans* >90 m tall at Wallaby Creek grew up to ~20 cm/yr, suggesting that even they had not yet achieved their maximum height (Sillett et al. 2010). Parameterized models suggested that wood mass production increased with tree size at Wallaby Creek, albeit at an ever decreasing proportional rate and representing energy harvest over an ever increasing area. Several stands in the Yarra Ranges and nearby originated after the highly

destructive Black Friday fires of 1939. *Eucalyptus regnans* established after those fires at one site had, when seen in 2007, achieved a maximum height of 82 m (Sillett et al. 2010), implying a growth rate of 1.2 m per year over nearly seven decades. This astonishing growth rate is accompanied by exceptionally slender stems, the production of notably light wood (ca. 425 kg/m<sup>3</sup>), with numerous thin-walled, large-diameter, long vessels (~280  $\mu\text{m} \times 1.8$  m) that frequently collapse when sawn wood is dried, and by strong xylem tapering that results in much of the axial resistance to water flow being confined to the last 1 m below the tree's apex, suggesting exceptionally shallow declines in  $\psi_{\text{leaf}}$  with height (Petit et al. 2010), as also seen in many conifers from temperate rain forests in the Pacific Northwest (McDowell et al. 2011).

These internal factors should clearly contribute to exceptional maximum heights in *Eucalyptus regnans*, the tallest angiosperm on Earth. Great stature is also favored by the relatively rich, fine-grained soils that *E. regnans* occupies in southern portions of the Great Dividing Range and its various subdivisions; the relatively high levels of P and major cations in these soils presumably reflect bedrock weathering and soil rejuvenation associated with orogeny (see Vitousek et al. 2003). Soils associated with *E. regnans* are typically rich in N, with high rates of N mineralization and high rates of N<sub>2</sub> fixation by associated *Acacia* immediately following disturbance by fire (Wang et al. 2008, Pfautsch et al. 2009, Tng et al. 2012), presumably facilitated by relatively high levels of soil P (Vitousek et al. 2010). The combination of relatively high soil fertility (Appendix: Figs. A2–A5) and a high ratio of precipitation to pan evaporation (Fig. 3), together with several decades to a few centuries between stand-destroying fires (Mifsud 2002, Tng et al. 2012), and the aforementioned internal traits help account for the great maximum height of *Eucalyptus regnans*. The tallest, recently alive individuals of this species on the Australian mainland were included in this study; the tallest anywhere occur slightly to the south, in Tasmania, under even higher  $P/E_p$  ratios (Tng et al. 2012).

It is remarkable that 8 of the 11 tallest tree species in the world are found in tall sclerophyll forests and adjacent temperate rain forests, including five conifers in the Pacific Northwest of the United States and four *Eucalyptus* species in Tasmania and Victoria in Australia (Tng et al. 2010). Only two occur in tropical rain forests, despite the warmer, rainier, and more humid conditions prevailing there. Why? Worldwide, rainfall of the wettest month appears to be the best predictor of tree height (Moles et al. 2009), but this metric fails to account for the distribution of the largest trees. Five reasons for the concentration of the tallest trees in tall sclerophyll forests and temperate rain forests vs. tropical rain forests seem plausible. First, the yearly thermal regimes of the former are more likely to maximize the difference between gross primary productivity (GPP)

and respiration than the latter; the tallest trees are indeed clustered in cool, often temperate maritime climates (Larjavaara 2013). Second, the much greater evaporative load placed on the tops of tree crowns by intense sunlight in the tropics should sharpen water potential gradients near tree apices and limit height growth. Third, the much higher rate of tree mortality in tropical forests (1.7% of canopy/yr [Stephenson and van Mantgem 2005]) compared with temperate rain forests (0.1–0.4% of canopy/yr) should reduce tree height in tropical vs. temperate rain forests. Such differences in mortality must be balanced against rates of primary productivity; in temperate rain forests, the latter can closely approach or exceed those of tropical rain forests (e.g.,  $3.6 \text{ kg}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  for *Eucalyptus regnans* [Attwill 1991]). Fourth, although tropical montane forests have favorable climates for GPP (Larjavaara 2013), we believe that their shallow, heavily leached, infertile soils (Tanner et al. 1998) and unstable steep slopes explain why the tallest trees are absent there. Finally, the shallow slope of  $\Delta$  vs. height in several gymnosperms (McDowell et al. 2011) and the hydraulic architecture of *Eucalyptus regnans* (Petit et al. 2010) suggest that these denizens of tall sclerophyll forests and temperate rain forests show exceptionally shallow declines in  $\psi_{\text{leaf}}$  with height, an internal factor that should also contribute to exceptional maximum tree heights.

The strong relationship between  $\ln(\text{maximum tree height})$  and  $\ln P/E_p$  seen in *Eucalyptus* along the Victoria transect is likely to be weaker in other areas, where greater genetic divergence among lineages, greater variation in other environmental conditions (e.g., temperature, length of growing season, average solar angle, soil depth) and in the rate of canopy-destroying disturbances, or less strong covariation of soils with climate could increase variance in realized tree height. Anyone who has, for example, seen 2 m tall *Cupressus goveniana* subsp. *pygmaea* and *Pinus contorta* subsp. *bolanderi* on thin, highly impoverished, periodically flooded soils growing immediately adjacent to 60-m tall *Sequoia sempervirens* on deeper, richer soils (Westman 1975) could not doubt the importance of substrate in determining maximum tree height. Nevertheless, the ties of tree height to  $P/E_p$ , and of  $\Delta$  to  $P/E_p$  and tree height described here are two of the first quantitative relationships relating tree height to environmental variables, and should now be explored in a variety of communities. The data on global variation in forest canopy height based on spaceborne lidar (Simard et al. 2011) would be an excellent starting point for such analyses.

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#### SUPPLEMENTARY MATERIAL

##### Ecological Archives

The Appendix is available online: <http://dx.doi.org/10.1890/14-0240.1.sm>