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Shoot growth of woody trees and shrubs is predicted by maximum plant height and associated traits

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Summary

1. The rate of elongation and thickening of individual branches (shoots) varies across plant species. This variation is important for the outcome of competition and other plant-plant interactions. Here we compared rates of shoot growth across 44 species from tropical, warm temperate, and cool temperate forests of eastern Australia.

2. Shoot growth rate was found to correlate with a suite of traits including the potential height of the species, xylem-specific conductivity, leaf size, leaf area per xylem cross-section, twig diameter (at 40 cm length), wood density and modulus of elasticity.

3. Within this suite of traits, maximum plant height was the clearest correlate of growth rates, explaining 50 to 67% of the variation in growth overall (p < 0.0001), and 23 to 32% of the variation (p < 0.05) in growth when holding the influence of the other traits constant. Structural equation models suggest that traits associated with ‘hydraulics’, ‘biomechanics’, and the ‘leaf economics spectrum’ represent three clearly separated axes of variation, with the hydraulic axis exhibiting the strongest alignment with height and largest independent contribution to growth (in the case of branch thickening). However most of the capacity of these axes to predict growth was also associated with maximum height, presumably reflecting coordinated selection on multiple traits that together influence life histories.

4. Growth rates were not strongly correlated with leaf nitrogen or leaf mass per unit leaf area.

5. Correlations between growth and maximum height arose both across latitude (47%, p < 0.0001) and from within-site differences between species (30%, p < 0.0001). Covariation between growth and maximum height was driven in part by variation in irradiance across sites as well as among canopy positions within sites (23%, p <
A significant fraction of this shared variation was independent of irradiance (45%, $p < 0.0001$), reflecting intrinsic differences across species and sites.

**Keywords** growth rate, plant traits, shoot extension, conductivity, leaf size, climate, structural equation modelling
Introduction

Plant growth rate varies markedly among plant species and is an important component of fitness in vegetative communities (Harper 1977). Faster growth rate may decrease the time to maturity, increase reproductive output through larger and more numerous propagules, or both (Harper 1980; Metcalf, Rose & Rees 2003). Growth also leads to increased plant height and size, which directly facilitates access to photosynthetically active radiation (PAR), water, nutrient resources, and reduces the susceptibility of the crown to fire and animal browsing. Perhaps most importantly, plants that can achieve greater stature through faster growth will intercept a much larger share of PAR than their shorter competitors. ‘Winners’ in the race for PAR may come to dominate communities. This is because PAR absorption in canopies is exponential, such that for a small increase in height, a plant may intercept a much larger proportion of PAR (Kira, Shinozaki & Hozumi 1969). Effectively, this results not only in taller plants accessing higher PAR environments, but also the removal of this resource for use by shorter competitors, i.e., variation in height results in asymmetric competition (Freckleton & Watkinson 2001). It is likely that this dynamic has resulted in the evolutionary divergence of height and PAR-use physiologies evident among extant forest species (Chapin, Autumn & Pugnaire 1993).

Measurements of plant growth need to be both accurate and ecologically meaningful, yet how best to measure growth remains an unresolved issue. The diameter growth of large forest trees can easily be measured, and with carefully calibrated allometric models, these measurements can be converted to mass and/or volume growth across a broad range of sites (Chave et al. 2014). Measuring plant growth via linear extension and diameter increase of terminal shoots also has advantages. Linear extension and diameter increase of terminal shoots can be measured directly and non-destructively on individual plants and represents an
ecologically relevant expression of the competitive race for height. As such, we suggest that
the linear extension of terminal shoots is a particularly meaningful assessment of a species’
ability to achieve height and reach high-radiation environments quickly.

This study assessed the influence of three plant functional processes on plant growth:
1) hydraulic processes that provide access to water and transport water to the sites of
photosynthesis and evaporation, 2) photochemical processes that convert water and CO₂ into
organic compounds, and 3) mechanical processes that lift photosynthetic tissues up into high
radiation environments, often at considerable expense to the plant, and provide support under
a diversity of stresses (Butler et al. 2011). Representative traits of each of these processes
should be correlated with plant growth. Hydraulic traits have been found to positively
correlate with growth in mature and juvenile tree species, including conduit diameter (Poorter
et al. 2010; Russo et al. 2010; Fan et al. 2012; Hoeber et al. 2014), leaf area per xylem cross-
section (Sterck et al. 2012), and xylem-specific conductivity (Kondoh et al. 2006; Poorter et
al. 2010; Fan et al. 2012; Hoeber et al. 2014). Growth of mature trees has also been found to
positively correlate with photosynthetic capacity (Prior, Eamus & Bowman 2004), nitrogen
and chlorophyll content of leaves (Prior, Eamus & Bowman 2004; Matzek & Vitousek 2009;
Hoeber et al. 2014) and leaf mass per unit leaf area (LMA) (Huante, Rincón & Acosta 1995;
Wright & Westoby 1999; Prior, Eamus & Bowman 2004). Perhaps the best known
representation of these correlated leaf traits is the ‘leaf economics spectrum’, whereby across-
species covariation in leaf lifespan, LMA, photosynthetic capacity, and nitrogen
concentration characterizes a species’ economic strategy – from slow to fast return on carbon
and nitrogen investments (Wright et al. 2004). Lastly, it has been suggested that wood
density, wood stiffness (modulus of elasticity; MOE), and mechanical safety in face of
gravity and wind may trade off against the capacity of xylem tissue to transport or store water
If this were true we might also expect inverse correlation between growth and the traits conferring mechanical safety, as has been found across tropical angiosperm species (King et al. 2006; Poorter et al. 2008; Hoeber et al. 2014; Iida et al. 2014).

It is important to realize that many traits that could potentially confer fast growth are beneficial only in high PAR environments. For example, increasing photosynthetic surface area should lead to faster growth, all else remaining equal. However, increasing leaf area also leads to greater self-shading and lower net CO₂ assimilation rate per unit leaf area (Sterck & Schieving 2011). Thus, species that invest in ‘leafier’ canopies, or higher photosynthetic capacity per unit leaf area, might achieve greater fitness in high PAR environments than they would in shaded environments. As an upshot, we might expect various growth traits (e.g., leaf area per xylem cross-section, LMA, A_max) to be aligned with one another, together with the achievable height of a species.

Here we address differences across species in the pace of extension growth, measured both as linear extension and as diameter increase, across 44 Australian woody angiosperm species (13 families) from three different sites, spanning 24 degrees latitude. We asked: 1) Does across-species variation in shoot growth correlate with variation in hydraulic, biomechanic or leaf economics traits? 2) Is the maximum attainable height of a plant correlated with the growth of terminal shoots, and if so, is the covariation between height and growth ‘bundled’ with other traits, or does it appear to be largely independent of other traits? 3) Are the dominant growth traits aligned with the PAR environment or with other site factors?
Materials and Methods

Species and sites

Three sites were chosen across a spread of latitude. A tropical site (-18.295, 145.492) was selected within Girringun National Park, about 80 km southeast of Mt. Garnet, Queensland, Australia. It was situated on a high level plateau (670 m asl), with warm wet summers and cool dry winters (MAP = 1106 mm, MAT = 21.3° C) (see Fig. S1 in Supporting Information). Tropical cyclones are common to this region, but the forest measured in this study did not exhibit signs of wind damage. A warm temperate site (-33.596, 151.285) was selected within Ku-ring-gai Chase National park, ca 20 km north of Sydney, Australia. The site was located on a broad gently sloping ridge (160 m asl) with a slight southeast aspect (MAP = 1192 mm, MAT = 17.0° C). A cool temperate site (-42.387, 147.048) was located on private property 1 km east of Bothwell, Tasmania, Australia, in gently rolling terrain of varying aspect (420 m asl) (MAP = 547 mm, MAT = 10.0° C). Sites were chosen to represent a range of mean annual temperatures and aridity. Aridity, calculated as the ratio of mean annual precipitation (MAP) to potential evapotranspiration (PET), was 0.60, 0.99, and 0.65 for the tropical, warm temperate, and cool temperate sites, respectively. Monthly precipitation, maximum temperature, and number of frost days varied considerably among sites (see Fig. S1). Soils were silica-rich and derived from sandstone (cool and warm temperate sites) or from deeply weathered lateritic surfaces (tropical). All sites were in open woodlands with diverse understory communities, a vegetation type common in eastern Australia and well-represented globally. None of the communities measured in this study exhibited signs of major disturbance (e.g., wind, fire, drought). All species measured were evergreen dicotyledons with the exception of two semi-drought-deciduous species at the tropical site: Lophostemon suaveolens and Planchonia careya.
The 12-16 most abundant species at each of the three sites were chosen for growth measurements (see Table S1). There were no species in common among sites. Between 11 and 20 mature individual plants, as close to their maximum height as possible, and of similar height, were chosen per species based on published descriptions (see Table S1). Access to species less than 3 m tall was achieved with ladders or from the ground, and species taller than 3 m were accessed using a hydraulic elevated lift (‘cherry picker’). For species with maximum height above 12 m, individuals 10-12 m in height were chosen, this being the upper limit of what could be reached with the lift. This sampling scheme resulted in sampled plant heights that were close to maximal heights for short species, but somewhat less than maximal for larger species (see Fig. S2). Five leader shoots were chosen from each individual plant and labelled with non-toxic paint and colored twist-ties at the start of the growth season in 2012 (late May at the tropical site, July at the warm temperate site, and October at the cool temperate site). Leader shoots were identified as branches near the apex of the canopy, unshaded by other branches, not suffering from substantial herbivory or physical damage, and exhibiting an upward growth trajectory, as opposed to growth directed sideways or towards the interior of the canopy. As our interest was in potential maximum growth, we took the most vigorous of the five shoots from each individual for subsequent analysis, i.e. the shoot with the largest length and diameter increment. Shoots were marked at the nearest branching point from the tip and the length between this branching point and the tip was measured to the nearest mm with a pliable tape measure, following the natural contours of the shoot. In addition, two perpendicular diameters were measured for each shoot 2 cm from the branching point to the nearest 0.01 mm with digital calipers. One year later these plants were revisited and re-measured, again at the start of the growth season (see dates above), yielding one year of extension and diameter growth on each measured shoot.
Shoot loss was also recorded, as well as the likely causes of loss (e.g. insect, wind, mammal). This information was the basis for choosing the most vigorous shoot on each plant (see below). Mean shoot extension values were calculated for each species.

Traits

As detailed in the introduction, a broad range of traits have been shown or hypothesized to correlate with growth. This study explored a range of traits likely to influence growth rates in adult plants. With the exception of wood density, \( A_{\text{max}} \), modulus of elasticity, and twig diameter, all traits were log transformed as this improved data normality. Traits were generally measured on different individual plants to those assessed for growth, e.g., shoot growth, leaf area per xylem cross-section, and MOE were measured on different individuals.

**Maximum height** for each species was taken from a previously published report (Gleason et al. 2012). Maximum height values were gathered from a variety of sources – field guide descriptions, herbarium specimen labels and field observations. As such, within-species error in maximum height was not measured.

**Leaf mass per area** (LMA) was determined by scanning 3-10 leaves from 5 individual plants, drying these leaves to constant mass at 70\(^\circ\) C, and expressing LMA as dry leaf mass divided by fresh leaf area. All leaves and shoots collected in this study were taken from the sun-lit upper canopies of mature plants, accessed either via ladder or elevated lift, as described above.

**Leaf area per xylem cross-section** (LA/XA) is the amount of leaf area supplied by a given xylem cross section. It represents investment in leaf area relative to investment in xylem area, and thus measures the degree to which a species places a premium on leaf allocation or water delivery. LA/XA is an important component of maximal leaf-specific conductivity, which is the product of LA/XA and the conductivity of the xylem tissue.
(xylem-specific conductivity; described below). LA/XA had been measured for many of the species previously (Gleason et al. 2012). Briefly, leader shoots were cut from five mature individuals of each species. Leaf mass, stem mass, and stem diameter underneath the bark were measured on each shoot at 5, 10, 20, 40, 80 and 120 cm from the tip. Leaf-mass per unit area (LMA; described above) was measured in these same individuals and used to convert leaf mass to leaf area. Allometric functions were fitted for each species relating leaf area to stem cross-sectional area (excluding bark) using the measurements at 5, 10, 20, 40, 80, and 120 cm. The ratio of leaf-area to xylem-area (inside-bark cross sectional area, minus pith) was estimated from these equations for each species at 1 cm diameter (Butler et al. 2011).

**Xylem-specific conductivity** was measured on one shoot from each of five mature individuals per species using a Sperry apparatus (Sperry, Donnelly & Tyree 1988), as described in Gleason et al (2012). Briefly, branch segments ranging in diameter from 0.3 to 0.7 cm (distal end of the segment) were cut to 80 cm in length underwater. Maximal conductance was measured across a 100 kPa pressure gradient using filtered (0.2 μm) and degassed 0.02 M KCL solution. Solution was collected and weighed to the nearest 0.00001 g (Satorius CP225D, Göttingen, Germany) and logged every 15 s to calculate flow rate. Xylem-specific conductivity was calculated by normalising the total segment conductance by the xylem cross sectional area, branch length and pressure gradient, and correcting for solution viscosity.

**Leaf size** was measured as the one-sided projected area of a leaf. Five to ten leaves from each of five plants were sampled and measured with a flatbed scanner. For the one species with compound leaves (*Acacia dealbata*), area of individual leaflets is reported. **Wood density** was calculated as oven-dried xylem mass divided by fresh xylem volume. Shoots similar to those measured for growth were collected from five individual
plants. Volume was measured using the mass-displacement method. The pieces were then oven-dried at 70°C and weighed (Gleason et al. 2012).

**Net CO₂ assimilation** under saturating PAR ($A_{\text{max}}$; $\mu$mol m$^{-2}$ s$^{-1}$) was measured in the field on five separate individuals per species with a portable LI-6400 photosynthesis system equipped with a 6400-02B LED light source (LI-Cor Biosciences, Lincoln, NE, USE). Saturating PAR values were chosen for each species by constructing a ‘step-down’ light response curve on the first individual. Saturating PAR varied from ca 400 to 2000 $\mu$mol m$^{-2}$ s$^{-1}$ across species. Reference CO₂, vapor pressure deficit (VPD), and temperature were kept within a narrow range across all measurements (388-402 ppm, 1.9-2.1 kPa, 23-27 °C, respectively) (Butler, Gleason & Westoby 2012).

**Leaf nitrogen** concentration was measured on dried green leaves from five individual plants per species, combined into one sample and analyzed for nitrogen as previously reported in Butler et al. (2012).

**Modulus of elasticity** (MOE) is a measurement of wood stiffness. Higher MOE values indicate stiffer wood. MOE is highly correlated with wood density, which represents a significant non-photosynthetic carbon sink. MOE was included in our trait analysis because it is an important component of stem stiffness and mechanical stability, and we were interested in evaluating a possible tradeoff between growth rate and mechanical safety, i.e., that faster growing species may achieve greater rates of shoot extension at the expense of wood stiffness. MOE was measured using a general materials testing machine (Model 5542; Instron Corporation, Canton, MA, USA) by performing a three-point bending test on fully hydrated stems with bark as previously reported in Butler et al. (2011).

**Saturated leaf water content** (SWC) is correlated with leaf tissue capacitance and is a significant source of water during desiccation in small plants and shoots (Gleason et al. 2014). Therefore, we considered SWC an important trait that could potentially influence
growth. SWC was measured on 3-5 leaves from 5 individual plants for each species. Fresh leaves were submerged in water at 20° C for 12 h. Leaves were then blotted dry, weighed on a laboratory balance, dried to constant mass at 70° C, and reweighed. SWC was calculated as the fraction of mass lost during drying (water mass) divided by the leaf dry mass.

**Twig diameter at 40 cm from the apex** was measured over bark on three to nine individuals of each species by averaging two perpendicular measurements of leader branches 40 cm back from the shoot tip. A significant correlation between twig diameter and shoot extension indicates that the ‘shape’ of shoots is an important factor influencing growth.

**Irradiance**

The irradiance environment was characterized above every plant for which extension and diameter growth was measured. One hemispherical photo was taken immediately above the center of each canopy using a self-leveling Nikon Coolpix 4500 camera with a Nikon FC-E8 fisheye converter. Hemispherical photos were taken concurrently with the final growth measurements. The captured images were processed using Gap Light Analyzer (Frazer, Canham & Lertzman 1999) to estimate the total fraction of short-wave radiation transmitted through the canopy directly over each measured plant during the course of a year, given latitude and azimuth, hereafter expressed as ‘irradiance’ (MJ m⁻² d⁻¹).

**Statistical analyses**

Bivariate correlations between growth and the 11 traits described above were first examined to identify key traits linked with growth. Partial correlations were then used to better understand the covariation structure among traits and to further identify which traits were associated with growth after partialling out the influence of the other traits. The ‘pcor.test’ function in the ppcor package for R was used for this analysis (Kim 2015). Exploratory
factor analysis was subsequently used to reduce the number of trait dimensions and to identify key axes of variation among traits that were also aligned with growth. The ‘esem’ function in the psych package for R was used for this analysis (Revelle 2016).

Maximum attainable height of a species was the only trait that explained significant (α = 0.05) variation in growth after partialling out the influence of the other traits. Furthermore, exploratory factor analysis revealed the clear separation of traits into three axes of variation – traits relating to hydraulic functioning, traits relating to mechanical safety, and traits relating to leaf economics. Informed from these results, structural equation models (SEM) were developed (described below) and tested using the ‘sem’ function in the lavaan package for R (Rosseel 2012). Structural equation modeling considers both measured and ‘latent’ variables. Latent variables are linear representations of groups of strongly correlated traits (i.e., the ‘hydraulic’, ‘biomechanic’, or the ‘LES’ factors). As such, each latent variable includes the variation in common among two or more measured traits, similar to scores on an obliquely rotated factor, and are presumed to represent a higher-order level of plant functioning, e.g., the hydrologic or biomechanic strategy of the species. Although it was clear from the exploratory factor analysis that three groups of strongly correlated traits (i.e., latent variables) emerged from the dataset, it was not known if all latent variables would be needed to predict variation in growth. Therefore, SEM was used to test if one, two, or all three of the latent variables (hydraulic, biomechanic, and LES trait groups) were necessary to accurately model growth. SEM was also used to test the direct effect of height on growth, as well as its influence via the measured and latent variables.

There are different opinions on how to best evaluate structural equation models. In this case we report the root mean square error of approximation (RMSEA), AIC, chi-sqr p value, and the comparative fit index. Better fitting models exhibit lower RMSEA, whereas lower AIC values may reflect better fit and/or greater regularization. Counterintuitively,
better fitting SEM models generally have lower chi-square values and higher associated p values than poorer fitting models. This is because the SEM null hypothesis assumes no difference between the observed data and the proposed model. Therefore, poorly specified SEM models are less congruent with the observed covariance matrix (i.e., higher chi-square values) than appropriately specified models. The comparative fit index (CFI) compares the fit of a specified model to a model where the variables are assumed to be uncorrelated. As such, CFI represents the difference in chi-square between the observed and predicted covariance matrices, with values closer to one indicating better fit. We point readers to Kline (2012) for discussion of the limitations and assumptions of SEM, as well as Belluau & Shipley (2017) (2017) and Grace (2008) for practical application of this method.

The first SEM model tested the direct influence of height on growth vs the indirect influence of height on growth, as manifested through the measured traits. For example, it is well-understood that plant size may influence volumetric and mass growth rate directly (Hunt 1978). However, it is also plausible that height (and access to direct radiation) is coordinated with other traits via natural selection (e.g., xylem-specific conductivity), and that growth is the outcome of these other coordinated traits, rather than height per se. The second model was the same as the first except that the indirect influence of height on growth was allowed only through each of the hydraulic, biomechanic, and LES latent variables. This makes sense if the evolution of height has been coordinated with the hydraulic or biomechanical strategies of species more generally, rather than with individual traits. The third and fourth models tested if all three latent variables were necessary, or if model fit improved meaningfully when some were removed. Model 3 included only the ‘hydraulic’ latent variable, whereas model 4 included both ‘hydraulic’ and ‘biomechanic’ latent variables.

Finally, we wanted to know if differences in irradiance and/or site (tropical, subtropical, temperate) significantly influenced the fitted slope and intercept coefficients of
the bivariate analyses. We used the base functions ‘aov’ and ‘TukeyHSD’ in R to fit slopes and assess mean separation among the sites, respectively (R Core Team 2015).

Results

Trait correlations

Species growth rates, measured as length extension or diameter increment of the most vigorous shoots on each plant, were correlated with a range of traits that included the maximum attainable height of the species, leaf size, leaf area per xylem cross-section, xylem-specific conductivity and twig diameter at 40 cm from the tip (Table 1). Although length and diameter increments could in principle give different signals – for example, if some species or individual shoots had more side-branching than others – they proved closely correlated ($R^2 = 0.81$) across the species examined here. Both measures of growth were similarly correlated with most of the traits examined, with the exception that only diameter growth was correlated with wood density and modulus of elasticity (Table 1). Only maximum height was significantly correlated with growth rates after partialling for all other traits (Table 2).

Further, only LMA and twig diameter remained significantly correlated with growth after partialling for maximum height ($p$ close to 0.05 in both cases) (Table S2).

Exploratory factor analysis revealed clear separation of traits into hydraulic, biomechanic, and LES traits (Table S3), as well as close association of height with the hydraulic trait factor (Table S3). Considering SEM models 1 and 2, model 2 provided a better fit, with the root mean square error of the approximation (RMSEA) decreasing from 0.194 to 0.032, and the AIC value decreasing from 958 to 906 (Table 3). This suggests that the latent variables were able to adequately represent the relevant variation in the measured traits, with the predictive capacity of both models for length and diameter growth being only moderately reduced in model 2 (Table 3). This reflects the large degree of multicollinearity
among the measured traits and supports the hypothesis that the measured traits align with a higher-order axis of variation reflecting plant strategy, and that plant height is the dominant trait associated with this axis. Evaluation of models 2, 3, and 4, revealed that the model including only the hydraulic latent variable (model 3) generally outperformed models including two or all three latent variables, with lower AIC and RMSEa values (Table 3). This suggests that plant traits aligned with the hydraulic factor are able to adequately predict variation in growth (extension and diameter growth $R^2 = 0.43$ and 0.61), without considering biomechanic or LES traits (Table 3). However, because the model including all three latent variables (model 2) provides a much better representation of how hydraulic, biomechanic, and LES traits relate to one another, as well as to height and growth, we have redrawn model 2 here (Fig 1). Standardized SEM coefficients represent the change in one variable relative to the change in another (in units of SD) whilst holding the influence of all other relevant variables constant. Although all the hydraulic traits exhibited strong correlation with growth by themselves (Table 1) this influence disappeared almost completely in the SEM because the predictive capacity of these variables was also aligned with the predictive capacity of height on growth. Thus, the ‘indirect’ effect of height through the latent variables was markedly weak, whereas the ‘direct’ effect of height on growth was strong (Fig. 1). For example, the coefficients between height and the hydraulic axis were 0.85, whereas the coefficients between the hydraulic axis and growth were weaker (-0.02, 0.25). This does not suggest that the latent variables are not correlated with growth, but that their contributions to growth were also closely aligned with variation in height.

Site effects

Species growth rates measured either as length or diameter increase were greatest at the tropical site (log transformed length growth $F_{2,41} = 21.11$, $p < 0.0001$; log transformed
diameter growth $F_{2,41} = 18.23, p < 0.0001)$. Mean length growth across species at each site varied from 7.83 mm y$^{-1}$ (SD = 4.19) at the warm temperate site, to 10.1 mm y$^{-1}$ (SD = 6.51) at the cool temperate site, to 36.2 mm y$^{-1}$ (SD = 18.1) at the tropical site. Similarly, mean diameter growth across species at each site varied from 1.00 mm y$^{-1}$ (SD = 0.67) at the warm temperate site, to 1.14 mm y$^{-1}$ (SD = 0.83) at the cool temperate site, to 4.53 mm y$^{-1}$ (SD = 2.43) at the tropical site. Several of the traits that correlated with growth rate also varied with latitude. Nevertheless, maximum height and most of the other traits significantly correlated with growth (Table 1) remained significant after site had been accounted for (see Table S5). In general, traits had a consistent relationship with growth across the sites; interaction terms were rarely significant (see Table S5). Site effects explained between 47% and 52% of the variance in growth rates, and a combination of plant functional traits explained up to an additional 30%. After accounting for site, maximum height explained 17% of the variance in length increase and 30% of the variance in diameter increase – a greater proportion than any other trait (Fig. 2, Table 4).

The question arises whether the observed correlation between growth rates and height was due to coordination between growth and maximum-height strategies, or simply as a response to taller plants benefiting from a more favorable irradiance environment. Species tended to be exposed to different irradiance environments both because of differences in irradiance between latitudes, and because of differences in canopy position within sites. However, there was no strong relationship between growth and irradiance either within or among sites in all cases (Fig. 3; $R^2 < 0.42$ and $p > 0.01$). Although irradiance did have some predictive capacity (linear models, Table 4), maximum height remained significant even after irradiance was included in the model, and explained 2 to 3 times as much of the variation in length and diameter growth rates (Table 4).
Discussion

Our evidence supports the hypothesis that growth of mature plants and their maximal height have been closely coordinated via natural selection, and that this axis of variation is also closely aligned with traits relating to water transport and leaf deployment. Traits tended to be better correlated with diameter growth than length growth, possibly because diameter growth captures growth in side branches as well as leader growth. Importantly, leaf traits including leaf nitrogen, LMA, $A_{\text{max}}$, and leaf saturated water content were not strongly correlated with observed shoot growth rates in these full-grown plants. Low LMA in particular has sometimes been treated as an indicator of fast growth strategies. It is indeed an indicator of fast growth during exponential seedling growth (Poorter & Remkes 1990; Wright & Westoby 1999) where low LMA confers low-cost deployment of leaf area. However, for plants with well-developed canopies, low LMA confers short leaf lifespan, which represents a significant turnover cost when leaves are replaced. Theory and meta-analyses indicate that correlations between growth and low LMA may break down or even reverse in plants that have developed large canopies with high rates of leaf turnover (Weemstra et al. 2013; van der Sande, Zuidema & Sterck 2015; Falster, Duursma & FitzJohn 2016; Gibert et al. 2016).

We found that xylem-specific conductivity and leaf area per xylem cross-section were also closely associated with the growth-height axis. Large deployment of leaf area per xylem cross-section might be expected to benefit growth (Poorter & Remkes 1990; Huante, Rincón & Acosta 1995; King 1997; Lusk, Contreras & Figueroa 1997; Reich 1998; King 2003; Sterck et al. 2012), particularly if it is coupled with efficient xylem tissue, having greater conductive capacity per unit cross-sectional area and length, i.e., greater xylem-specific conductivity (Gleason et al. 2012). As such, our study supports the hypothesis that efficient xylem may have facilitated the evolution of tall plants, leafy shoots, and fast growth in environments with high PAR and high precipitation.
The size of individual leaves was also found to be an important trait correlated with growth and maximal plant height. In part, this may have been because species with larger leaves tend to deploy them more efficiently on the shoot (Pickup, Westoby & Basden 2005; Wright et al. 2006) and to experience less within-shoot self-shading (Falster & Westoby 2003a). Leaf size has also been found to correlate with ‘leafiness’ and twig size (Ackerly & Donoghue 1998; Falster & Westoby 2003a; Westoby & Wright 2003; Kleiman & Aarssen 2007), which are related via ‘Corner’s rules’ (White 1983). As a consequence of their wider dimensions, however, larger leaves should have a tendency to overheat more than small leaves, assuming the components of energy balance are similar (Monteith & Unsworth 1990). To compensate for this, larger leaves may require a greater investment in transpirational capacity (i.e., a greater capacity for evaporative cooling). We might therefore expect xylem-specific conductivity to be linked with leaf size, as well as leaf area to xylem area ratio, to supply this additional transpiration. To the extent that xylem-specific conductivity may reflect transpirational capacity, our results support this hypothesis.

A number of studies have found a positive relationship between maximum height and RGR in forests (Sterck & Bongers 2001; Poorter et al. 2008; Martínez-Vilalta et al. 2010; Wright et al. 2010; Iida et al. 2014). Wright et al. (2010) observed that maximum height was part of a suite of traits, including wood density and leaf mass per area, that correlated with the relative growth rate of tropical tree species. Our study is unique in that it not only emphasises the importance of growth-height relationships across a much broader range of species and environments, but also suggests an evolutionary alignment of height and growth with water transport and leaf deployment traits. Although data reported here and elsewhere support correlation between height and growth, the mechanisms underpinning this correlation are not clear. Taller plants might have higher rates of growth for physiological reasons. Taller species are likely to sit higher in the canopy profile and intercept more PAR (Sterck &
Bongers 2001; King 2003; Poorter et al. 2008). Conversely, height might be expected to have a negative effect on carbon budget via increased xylem and bark (including phloem) maintenance costs (Givnish 1988; Falster & Westoby 2003b). Other ecological benefits of being tall, such as escaping fire (Higgins, Bond & Trollope 2000; Bond, Cook & Williams 2012) and browsing (Allcock & Hik 2004), are only gained once a height threshold has been reached, suggesting that the drivers for these benefits may select for both fast growth and tall stature.

Greater height may also be a detriment to forest species. Taller plants must transport water farther and higher than other species, resulting in increasing water tension in leaf and twig xylem, and possibly, higher incidence of embolism, and lower rates of stomatal conductance and photosynthesis (Ryan et al. 2000; Schäfer, Oren & Tenhunen 2000; Koch et al. 2004; Domec et al. 2008). Mortality rates have not been found to correlate with maximum height in most cases (Wright et al. 2010, Poorter et al 2008), but they may if mechanical safety also declines with height (Iida et al. 2014). It has also been reported that traits conferring fast growth may result in higher rates of damage from arthropods (i.e. growth rate hypothesis, Stamp 2003) and may also result in increased susceptibility to damage from falling or wind-driven debris (Clark & Clark 1991; Gleason et al. 2008).

Conversely, small statured species may grow more slowly because they invest in defense and seed production, therefore benefiting from lower mortality and higher fecundity (Wenk & Falster 2015).

In summary, shoot growth across the species and climates examined in this study was correlated with a suite of traits, including maximum height, xylem-specific conductivity, leaf area to xylem area ratio, leaf size, wood density, stem stiffness, and access to PAR, but with the important caveat that maximum height accounted for a significant amount of variation in growth that was independent of variation in the other traits. Taken together, height and
growth appear to be closely aligned via natural selection with the hydraulic and biomechanical functioning of wood and leaves. This result also suggests that natural selection has resulted in the near-complete confounding of the independent influence of xylem, leaf, and allometric traits on growth. Considering the marked collinearity among height and growth traits, it will be difficult to dissect the independent influences of traits on growth. Species that do not exhibit marked correlation among height and growth traits, i.e., species with large residuals from our fitted models, may represent opportunities to better understand why correlation among these traits exists, and under what circumstances this correlation might weaken. Genetically modified genotypes (e.g., “knockouts”) might also facilitate the investigation of growth–trait relationships independent of height and other closely allied traits.

Authors' Contributions

All authors contributed equally to ideas, methodology, data collection, and writing of the manuscript.

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Data Accessibility

Data deposited in the Dryad Digital Repository: http://doi.org/10.5061/dryad.tv652
Literature cited


Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix 1  R code for structural equation models
Figure S1  Mean monthly climate data for all sites
Figure S2  Maximum height recorded of species taken from the literature plotted against measured height.
Table S1  Species list
Table S2  Correlation between diameter or length growth and various traits after partialling for the effect of maximum height
Table S3  Exploratory factor analysis trait loadings
Table S4  Structural equation model syntax and associated hypotheses
Table S4  Analyses of covariation for length and diameter increments in relation to site location and traits

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Figure Legends

Fig. 1. Structural equation models representing the hypothesized trait networks associated with length extension (A) and diameter growth (B) of terminal shoots. Correlative relationships are denoted with double-headed arrows, whereas functional relationships are denoted with single-headed arrows. Standardized coefficients are given. Boxes represent measured traits, whereas circles represent latent variables (i.e., non-orthogonal factors). Latent variables are labeled ‘Hyd’ (hydraulics), ‘Bio’ (biomechanics), and ‘LES’ (leaf economics spectrum) and are linear manifestations of their corresponding traits. Ks = xylem-specific conductivity. LS = leaf area of an individual leaf. LX = leaf area supported by a given area of xylem cross section. TD = measured diameter of growing shoot at 40cm from the shoot tip. MOE = modulus of elasticity. WD = wood density. LMA = dry leaf mass / fresh green area. SWC = saturated water content of green leaves. LN = leaf nitrogen concentration of green leaves. Correlation between LS and LX was allowed because this should be expected to arise via ‘Corner’s Rules’. Similarly, the correlative relationship between WD and MOE is also well-understood (Evans & Ilic 2001) and has been included. The model drawn here (i.e., model 2 in Table 3) does not represent the ‘best-fit’ model, but is drawn to display the relationships among the traits more generally (i.e., better fitting models include fewer traits). Model fit and hypothesis testing are reported in Table 3.

Fig. 2  Growth increments as measured by length increase (A) and diameter increase (B) of vigorous shoots in relation to maximum height. Each symbol denotes a mean for a single species. Fitted lines represent significantly different intercepts among sites ($p < 0.0001$) and common slope coefficients, i.e., interaction terms were not significant in ANCOVA (see Table S1). Sites are denoted by the following symbols: Tropical (+), Warm temperate (△), and Cool temperate (○).

Fig. 3  Rates of length (A) and diameter (B) increase in relation to irradiance, measured as the mean total fraction of short-wave radiation transmitted through the canopy directly over
each species during the course of a year. Sites are denoted by the following symbols: Tropical (+), Warm temperate (△), and Cool temperate (〇).
Table 1. Pearson correlation $r$ (lower left-hand side of table) and $p$ values (upper right-hand side of the table) of all pairwise correlations. Significant correlations ($p \leq 0.05$) are shown in bold. Length growth = maximum length growth increment. Diam. Growth = maximum diameter growth increment. Max height = maximum height of species. Leaf area / xylem area = leaf area supported by a given area of xylem cross section. Leaf area = leaf area of an individual leaf. Wood density = wood density of growing shoots. $A_{\text{max}}$ = net CO$_2$ assimilation under saturating PAR. Leaf N = leaf nitrogen concentration of green leaves. LMA = dry leaf mass / fresh green area. Leaf SWC = water content / dry leaf mass. Stem (twig) diam = measured diameter of growing shoot at 40cm from the shoot tip. Irrad = the mean total fraction of short-wave radiation transmitted through the canopy directly over each species during the course of a year.

<table>
<thead>
<tr>
<th></th>
<th>Length growth (log)</th>
<th>Diam growth (log)</th>
<th>Max height (log)</th>
<th>Leaf-area / xylem-area (log)</th>
<th>Xylem-specific cond. (log)</th>
<th>Leaf area (log)</th>
<th>Wood density</th>
<th>Amax</th>
<th>Leaf N (log)</th>
<th>MOE</th>
<th>LMA (log)</th>
<th>leaf SWC (log)</th>
<th>Stem (twig) diam</th>
<th>Irrad</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of species measured</td>
<td>44</td>
<td>44</td>
<td>44</td>
<td>36</td>
<td>35</td>
<td>44</td>
<td>37</td>
<td>36</td>
<td>38</td>
<td>44</td>
<td>38</td>
<td>44</td>
<td>38</td>
<td>44</td>
</tr>
</tbody>
</table>
Table 2. Partial correlations between growth (diameter and length) and each of the 11 traits while holding the influence of the other traits constant. This analysis includes 34 species for which a complete set of traits (without missing observations) is available. Significant correlations (p ≤ 0.05) are shown in bold. Trait descriptions are the same as in Table 1.

<table>
<thead>
<tr>
<th></th>
<th>Max height (log)</th>
<th>Leaf-area / xylem-area (log)</th>
<th>Xylem-specific cond. (log)</th>
<th>Leaf area (log)</th>
<th>Wood density</th>
<th>Amax</th>
<th>Leaf N (log)</th>
<th>MOE</th>
<th>LMA (log)</th>
<th>leaf SWC (log)</th>
<th>Stem (twig) diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diameter growth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>r</td>
<td><strong>0.475</strong></td>
<td>0.052</td>
<td>0.210</td>
<td>-0.144</td>
<td>0.120</td>
<td>-0.272</td>
<td>-0.172</td>
<td>-0.064</td>
<td>0.039</td>
<td>0.204</td>
<td>0.239</td>
</tr>
<tr>
<td>p-value</td>
<td>0.012</td>
<td>0.807</td>
<td>0.314</td>
<td>0.494</td>
<td>0.572</td>
<td>0.185</td>
<td>0.412</td>
<td>0.762</td>
<td>0.855</td>
<td>0.328</td>
<td>0.249</td>
</tr>
<tr>
<td>Length growth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>r</td>
<td><strong>0.565</strong></td>
<td>-0.171</td>
<td>0.219</td>
<td>-0.240</td>
<td>0.281</td>
<td>-0.280</td>
<td>-0.203</td>
<td>-0.025</td>
<td>-0.147</td>
<td>0.267</td>
<td>0.199</td>
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<tr>
<td>p-value</td>
<td>0.001</td>
<td>0.417</td>
<td>0.293</td>
<td>0.247</td>
<td>0.170</td>
<td>0.172</td>
<td>0.330</td>
<td>0.909</td>
<td>0.486</td>
<td>0.193</td>
<td>0.340</td>
</tr>
</tbody>
</table>
Table 3. Fit statistics for all structural equation models. Model 1 (hypothesis 1) allows for the direct influence of height on growth, as well as indirect influence through the measured traits. Model 1 includes no latent variables – only measured traits. Model 2 (hypothesis 2) also allows for the direct influence of height on growth, but indirect influence is allowed only through latent variables ‘Hyd’, ‘Bio’, and ‘LES’, representing traits associated with hydraulic, biomechanical, and leaf economic spectrum traits, respectively. Model 2 is represented in Figure 1. Models 3 and 4 have similar model structure as model 2, except with reduced numbers of latent and measured variables. Model 3 includes only traits associated with the latent variable ‘Hyd’ and omits latent variables ‘Bio’ and ‘LES’, as well as their corresponding measured traits. Model 4 includes both latent variables ‘Hyd’ and ‘Bio’, but eliminates latent variable ‘LES’ as well as its associated traits. Total model fit improves with increasing p, CFI (comparative fit index), and with decreasing RMSEa and AIC values. The predictive capacity on growth (Growth R²) is also reported. The hypothesis structure and testing procedure are described in greater detail in the Supporting Information (Table S4). The R code used to perform the analyses is also published in the Supporting Information (see Appendix 1).

<table>
<thead>
<tr>
<th>Length growth</th>
<th>Model number</th>
<th>p (chi-square)</th>
<th>CFI</th>
<th>RMSEa</th>
<th>RMSEa upper CL</th>
<th>RMSEa lower CL</th>
<th>Growth r²</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>&lt; 0.001</td>
<td>0.654</td>
<td>0.233</td>
<td>0.288</td>
<td>0.179</td>
<td>0.652</td>
<td>950</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.210</td>
<td>0.963</td>
<td>0.073</td>
<td>0.147</td>
<td>&lt; 0.001</td>
<td>0.484</td>
<td>891</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.897</td>
<td>1.000</td>
<td>&lt; 0.001</td>
<td>0.127</td>
<td>&lt; 0.001</td>
<td>0.433</td>
<td>376</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0.610</td>
<td>1.000</td>
<td>&lt; 0.001</td>
<td>0.141</td>
<td>&lt; 0.001</td>
<td>0.442</td>
<td>628</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Diameter growth</th>
<th>Model number</th>
<th>p (chi-square)</th>
<th>CFI</th>
<th>RMSEa</th>
<th>RMSEa upper CL</th>
<th>RMSEa lower CL</th>
<th>Growth r²</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>&lt; 0.001</td>
<td>0.670</td>
<td>0.233</td>
<td>0.288</td>
<td>0.179</td>
<td>0.684</td>
<td>938</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.312</td>
<td>0.981</td>
<td>0.054</td>
<td>0.136</td>
<td>&lt; 0.001</td>
<td>0.639</td>
<td>876</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.932</td>
<td>1.000</td>
<td>&lt; 0.001</td>
<td>0.080</td>
<td>&lt; 0.001</td>
<td>0.614</td>
<td>361</td>
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<tr>
<td></td>
<td>4</td>
<td>0.707</td>
<td>1.000</td>
<td>&lt; 0.001</td>
<td>0.125</td>
<td>&lt; 0.001</td>
<td>0.638</td>
<td>611</td>
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</table>
Table 4. Linear models predicting growth (length and diameter) from irradiance followed by maximum species height. R² values calculated from sums of squares. Irradiance was calculated as the mean total fraction of short-wave radiation transmitted through the canopy directly over each species during the course of a year.

<table>
<thead>
<tr>
<th>Variable</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length growth (log) ~ Irradiance × Maximum height (log)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Irradiance</td>
<td>1</td>
<td>0.86</td>
<td>0.86</td>
<td>9.38</td>
<td>0.0045</td>
<td>0.14</td>
</tr>
<tr>
<td>Maximum height (log)</td>
<td>1</td>
<td>2.51</td>
<td>2.51</td>
<td>27.52</td>
<td>&lt; 0.0001</td>
<td>0.40</td>
</tr>
<tr>
<td>Irradiance × Maximum height (log)</td>
<td>1</td>
<td>0.06</td>
<td>0.06</td>
<td>0.65</td>
<td>0.4268</td>
<td>0.01</td>
</tr>
<tr>
<td>Residuals</td>
<td>31</td>
<td>2.83</td>
<td>0.09</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diameter growth (log) ~ Irradiance × Maximum height (log)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Irradiance</td>
<td>1</td>
<td>1.52</td>
<td>1.52</td>
<td>21.54</td>
<td>&lt; 0.0001</td>
<td>0.23</td>
</tr>
<tr>
<td>Maximum height (log)</td>
<td>1</td>
<td>2.98</td>
<td>2.98</td>
<td>42.33</td>
<td>&lt; 0.0001</td>
<td>0.45</td>
</tr>
<tr>
<td>Irradiance × Maximum height (log)</td>
<td>1</td>
<td>0.00</td>
<td>0.00</td>
<td>0.04</td>
<td>0.8481</td>
<td>0.00</td>
</tr>
<tr>
<td>Residuals</td>
<td>31</td>
<td>2.18</td>
<td>0.07</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Fig. 3

(A) Length increase (cm) vs. Irradiance (MJ m⁻² d⁻¹)

(B) Diameter increase (cm) vs. Irradiance (MJ m⁻² d⁻¹)

Legend:
- Cool: $r^2 = 0.38$, $p = 0.019$
- Warm: $r^2 = 0.35$, $p = 0.021$
- Tropical