1 **Shoot growth of woody trees and shrubs is predicted by maximum plant height and**

2 **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%, $p <$

48   0.0001). A significant fraction of this shared variation was independent of irradiance

49   (45%, $p < 0.0001$), reflecting intrinsic differences across species and sites.

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53

54   **Introduction**

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56   Plant growth rate varies markedly among plant species and is an important component of

57   fitness in vegetative communities (Harper 1977). Faster growth rate may decrease the time to

58   maturity, increase reproductive output through larger and more numerous propagules, or both

59   (Harper 1980; Metcalf, Rose & Rees 2003). Growth also leads to increased plant height and

60   size, which directly facilitates access to photosynthetically active radiation (PAR), water,

61   nutrient resources, and reduces the susceptibility of the crown to fire and animal browsing.

62   Perhaps most importantly, plants that can achieve greater stature through faster growth will

63   intercept a much larger share of PAR than their shorter competitors. 'Winners' in the race for

64   PAR may come to dominate communities. This is because PAR absorption in canopies is

65   exponential, such that for a small increase in height, a plant may intercept a much larger

66   proportion of PAR (Kira, Shinozaki & Hozumi 1969). Effectively, this results not only in

67   taller plants accessing higher PAR environments, but also the removal of this resource for use

68   by shorter competitors, i.e., variation in height results in asymmetric competition (Freckleton

69   & Watkinson 2001). It is likely that this dynamic has resulted in the evolutionary divergence

70   of height and PAR-use physiologies evident among extant forest species (Chapin, Autumn &

71   Pugnaire 1993).

72   Measurements of plant growth need to be both accurate and ecologically meaningful,

73   yet how best to measure growth remains an unresolved issue. The diameter growth of large

74   forest trees can easily be measured, and with carefully calibrated allometric models, these

75   measurements can be converted to mass and/or volume growth across a broad range of sites

76   (Chave *et al.* 2014). Measuring plant growth via linear extension and diameter increase of

77   terminal shoots also has advantages. Linear extension and diameter increase of terminal

78   shoots can be measured directly and non-destructively on individual plants and represents an

4

79   ecologically relevant expression of the competitive race for height. As such, we suggest that

80   the linear extension of terminal shoots is a particularly meaningful assessment of a species'

81   ability to achieve height and reach high-radiation environments quickly.

82   This study assessed the influence of three plant functional processes on plant growth:

83   1) hydraulic processes that provide access to water and transport water to the sites of

84   photosynthesis and evaporation, 2) photochemical processes that convert water and CO_2 into

85   organic compounds, and 3) mechanical processes that lift photosynthetic tissues up into high

86   radiation environments, often at considerable expense to the plant, and provide support under

87   a diversity of stresses (Butler *et al.* 2011). Representative traits of each of these processes

88   should be correlated with plant growth. Hydraulic traits have been found to positively

89   correlate with growth in mature and juvenile tree species, including conduit diameter (Poorter

90   *et al.* 2010; Russo *et al.* 2010; Fan *et al.* 2012; Hoeber *et al.* 2014), leaf area per xylem cross-

91   section (Sterck *et al.* 2012), and xylem-specific conductivity (Kondoh *et al.* 2006; Poorter *et*

92   *al.* 2010; Fan *et al.* 2012; Hoeber *et al.* 2014). Growth of mature trees has also been found to

93   positively correlate with photosynthetic capacity (Prior, Eamus & Bowman 2004), nitrogen

94   and chlorophyll content of leaves (Prior, Eamus & Bowman 2004; Matzek & Vitousek 2009;

95   Hoeber *et al.* 2014) and leaf mass per unit leaf area (LMA) (Huante, Rincón & Acosta 1995;

96   Wright & Westoby 1999; Prior, Eamus & Bowman 2004). Perhaps the best known

97   representation of these correlated leaf traits is the 'leaf economics spectrum', whereby across-

98   species covariation in leaf lifespan, LMA, photosynthetic capacity, and nitrogen

99   concentration characterizes a species' economic strategy – from slow to fast return on carbon

100   and nitrogen investments (Wright *et al.* 2004). Lastly, it has been suggested that wood

101   density, wood stiffness (modulus of elasticity; MOE), and mechanical safety in face of

102   gravity and wind may trade off against the capacity of xylem tissue to transport or store water

103   (Wagner, Ewers & Davis 1998; Sperry, Meinzer & McCulloh 2008; Pratt & Jacobsen 2016).

104   If this were true we might also expect inverse correlation between growth and the traits

105   conferring mechanical safety, as has been found across tropical angiosperm species (King *et*

106   *al.* 2006; Poorter *et al.* 2008; Hoeber *et al.* 2014; Iida *et al.* 2014).

107   It is important to realize that many traits that could potentially confer fast growth are

108   beneficial only in high PAR environments. For example, increasing photosynthetic surface

109   area should lead to faster growth, all else remaining equal. However, increasing leaf area

110   also leads to greater self-shading and lower net CO_2 assimilation rate per unit leaf area

111   (Sterck & Schieving 2011). Thus, species that invest in 'leafier' canopies, or higher

112   photosynthetic capacity per unit leaf area, might achieve greater fitness in high PAR

113   environments than they would in shaded environments. As an upshot, we might expect

114   various growth traits (e.g., leaf area per xylem cross-section, LMA, A_{max}) to be aligned with

115   one another, together with the achievable height of a species.

116   Here we address differences across species in the pace of extension growth,

117   measured both as linear extension and as diameter increase, across 44 Australian woody

118   angiosperm species (13 families) from three different sites, spanning 24 degrees latitude. We

119   asked: 1) Does across-species variation in shoot growth correlate with variation in hydraulic,

120   biomechanic or leaf economics traits? 2) Is the maximum attainable height of a plant

121   correlated with the growth of terminal shoots, and if so, is the covariation between height and

122   growth 'bundled' with other traits, or does it appear to be largely independent of other traits?

123   3) Are the dominant growth traits aligned with the PAR environment or with other site

124   factors?

125

126 **Materials and Methods**

127 Species and sites

128 Three sites were chosen across a spread of latitude. A tropical site (-18.295, 145.492) was

129 selected within Girringun National Park, about 80 km southeast of Mt. Garnet, Queensland,

130 Australia. It was situated on a high level plateau (670 m asl), with warm wet summers and

131 cool dry winters (MAP = 1106 mm, MAT = 21.3° C) (see Fig. S1 in Supporting

132 Information). Tropical cyclones are common to this region, but the forest measured in this

133 study did not exhibit signs of wind damage. A warm temperate site (-33.596, 151.285) was

134 selected within Ku-ring-gai Chase National park, ca 20 km north of Sydney, Australia. The

135 site was located on a broad gently sloping ridge (160 m asl) with a slight southeast aspect

136 (MAP = 1192 mm, MAT = 17.0° C). A cool temperate site (-42.387, 147.048) was located

137 on private property 1 km east of Bothwell, Tasmania, Australia, in gently rolling terrain of

138 varying aspect (420 m asl) (MAP = 547 mm, MAT = 10.0° C). Sites were chosen to

139 represent a range of mean annual temperatures and aridity. Aridity, calculated as the ratio of

140 mean annual precipitation (MAP) to potential evapotranspiration (PET), was 0.60, 0.99, and

141 0.65 for the tropical, warm temperate, and cool temperate sites, respectively. Monthly

142 precipitation, maximum temperature, and number of frost days varied considerably among

143 sites (see Fig. S1). Soils were silica-rich and derived from sandstone (cool and warm

144 temperate sites) or from deeply weathered lateritic surfaces (tropical) . All sites were in open

145 woodlands with diverse understory communities, a vegetation type common in eastern

146 Australia and well-represented globally. None of the communities measured in this study

147 exhibited signs of major disturbance (e.g., wind, fire, drought). All species measured were

148 evergreen dicotyledons with the exception of two semi-drought-deciduous species at the

149 tropical site: *Lophostemon suaveolens* and *Planchonia careya*.

150

151 Shoot extension

152 The 12-16 most abundant species at each of the three sites were chosen for growth

153 measurements (see Table S1). There were no species in common among sites. Between 11

154 and 20 mature individual plants, as close to their maximum height as possible, and of similar

155 height, were chosen per species based on published descriptions (see Table S1). Access to

156 species less than 3 m tall was achieved with ladders or from the ground, and species taller

157 than 3 m were accessed using a hydraulic elevated lift ('cherry picker'). For species with

158 maximum height above 12 m, individuals 10-12 m in height were chosen, this being the

159 upper limit of what could be reached with the lift. This sampling scheme resulted in sampled

160 plant heights that were close to maximal heights for short species, but somewhat less than

161 maximal for larger species (see Fig. S2). Five leader shoots were chosen from each

162 individual plant and labelled with non-toxic paint and colored twist-ties at the start of the

163 growth season in 2012 (late May at the tropical site, July at the warm temperate site, and

164 October at the cool temperate site). Leader shoots were identified as branches near the apex

165 of the canopy, unshaded by other branches, not suffering from substantial herbivory or

166 physical damage, and exhibiting an upward growth trajectory, as opposed to growth directed

167 sideways or towards the interior of the canopy. As our interest was in potential maximum

168 growth, we took the most vigorous of the five shoots from each individual for subsequent

169 analysis, i.e. the shoot with the largest length and diameter increment. Shoots were marked at

170 the nearest branching point from the tip and the length between this branching point and the

171 tip was measured to the nearest mm with a pliable tape measure, following the natural

172 contours of the shoot. In addition, two perpendicular diameters were measured for each

173 shoot 2 cm from the branching point to the nearest 0.01 mm with digital calipers. One year

174 later these plants were revisited and re-measured, again at the start of the growth season (see

175 dates above), yielding one year of extension and diameter growth on each measured shoot.

176 Shoot loss was also recorded, as well as the likely causes of loss (e.g. insect, wind, mammal).

177 This information was the basis for choosing the most vigorous shoot on each plant (see

178 below). Mean shoot extension values were calculated for each species.

179

180 Traits

181 As detailed in the introduction, a broad range of traits have been shown or hypothesized to

182 correlate with growth. This study explored a range of traits likely to influence growth rates in

183 adult plants. With the exception of wood density, A_{max}, modulus of elasticity, and twig

184 diameter, all traits were log transformed as this improved data normality. Traits were

185 generally measured on different individual plants to those assessed for growth, e.g., shoot

186 growth, leaf area per xylem cross-section, and MOE were measured on different individuals.

187 **Maximum height** for each species was taken from a previously published report

188 (Gleason *et al.* 2012). Maximum height values were gathered from a variety of sources –

189 field guide descriptions, herbarium specimen labels and field observations. As such, within-

190 species error in maximum height was not measured.

191 **Leaf mass per area** (LMA) was determined by scanning 3-10 leaves from 5

192 individual plants, drying these leaves to constant mass at 70° C, and expressing LMA as dry

193 leaf mass divided by fresh leaf area. All leaves and shoots collected in this study were taken

194 from the sun-lit upper canopies of mature plants, accessed either via ladder or elevated lift, as

195 described above.

196 **Leaf area per xylem cross-section** (LA/XA) is the amount of leaf area supplied by a

197 given xylem cross section. It represents investment in leaf area relative to investment in

198 xylem area, and thus measures the degree to which a species places a premium on leaf

199 allocation or water delivery. LA/XA is an important component of maximal leaf-specific

200 conductivity, which is the product of LA/XA and the conductivity of the xylem tissue

9

201 (xylem-specific conductivity; described below). LA/XA had been measured for many of the

202 species previously (Gleason *et al.* 2012). Briefly, leader shoots were cut from five mature

203 individuals of each species. Leaf mass, stem mass, and stem diameter underneath the bark

204 were measured on each shoot at 5, 10, 20, 40, 80 and 120 cm from the tip. Leaf-mass per

205 unit area (LMA; described above) was measured in these same individuals and used to

206 convert leaf mass to leaf area. Allometric functions were fitted for each species relating leaf

207 area to stem cross-sectional area (excluding bark) using the measurements at 5, 10, 20, 40,

208 80, and 120 cm. The ratio of leaf-area to xylem-area (inside-bark cross sectional area, minus

209 pith) was estimated from these equations for each species at 1 cm diameter (Butler *et al.*

210 2011).

211   **Xylem-specific conductivity** was measured on one shoot from each of five mature

212 individuals per species using a Sperry apparatus (Sperry, Donnelly & Tyree 1988), as

213 described in Gleason et al (2012). Briefly, branch segments ranging in diameter from 0.3 to

214 0.7 cm (distal end of the segment) were cut to 80 cm in length underwater. Maximal

215 conductance was measured across a 100 kPa pressure gradient using filtered (0.2 μm) and

216 degassed 0.02 M KCL solution. Solution was collected and weighed to the nearest 0.00001 g

217 (Satorius CP225D, Göttingen, Germany) and logged every 15 s to calculate flow rate.

218 Xylem-specific conductivity was calculated by normalising the total segment conductance by

219 the xylem cross sectional area, branch length and pressure gradient, and correcting for

220 solution viscosity.

221   **Leaf size** was measured as the one-sided projected area of a leaf. Five to ten leaves

222 from each of five plants were sampled and measured with a flatbed scanner. For the one

223 species with compound leaves (*Acacia dealbata*), area of individual leaflets is reported.

224   **Wood density** was calculated as oven-dried xylem mass divided by fresh xylem

225 volume. Shoots similar to those measured for growth were collected from five individual

226 plants. Volume was measured using the mass-displacement method. The pieces were then

227 oven-dried at 70°C and weighed (Gleason *et al.* 2012).

228 **Net CO₂ assimilation** under saturating PAR (A_{max}; $\mu mol\ m^{-2}\ s^{-1}$) was measured in the

229 field on five separate individuals per species with a portable LI-6400 photosynthesis system

230 equipped with a 6400-02B LED light source (LI-Cor Biosciences, Lincoln, NE, USE).

231 Saturating PAR values were chosen for each species by constructing a 'step-down' light

232 response curve on the first individual. Saturating PAR varied from ca 400 to 2000 $\mu mol\ m^{-2}$

233 s^{-1} across species. Reference CO_2, vapor pressure deficit (VPD), and temperature were kept

234 within a narrow range across all measurements (388-402 ppm, 1.9-2.1 kPa, 23-27 °C,

235 respectively) (Butler, Gleason & Westoby 2012).

236 **Leaf nitrogen** concentration was measured on dried green leaves from five individual

237 plants per species, combined into one sample and analyzed for nitrogen as previously

238 reported in Butler et al. (2012).

239 **Modulus of elasticity** (MOE) is a measurement of wood stiffness. Higher MOE

240 values indicate stiffer wood. MOE is highly correlated with wood density, which represents

241 a significant non-photosynthetic carbon sink. MOE was included in our trait analysis

242 because it is an important component of stem stiffness and mechanical stability, and we were

243 interested in evaluating a possible tradeoff between growth rate and mechanical safety, i.e.,

244 that faster growing species may achieve greater rates of shoot extension at the expense of

245 wood stiffness. MOE was measured using a general materials testing machine (Model 5542;

246 Instron Corporation, Canton, MA, USA) by performing a three-point bending test on fully

247 hydrated stems with bark as previously reported in Butler et al. (2011).

248 **Saturated leaf water content** (SWC) is correlated with leaf tissue capacitance and is

249 a significant source of water during desiccation in small plants and shoots (Gleason *et al.*

250 2014). Therefore, we considered SWC an important trait that could potentially influence

251 growth. SWC was measured on 3-5 leaves from 5 individual plants for each species. Fresh

252 leaves were submerged in water at 20° C for 12 h. Leaves were then blotted dry, weighed on

253 a laboratory balance, dried to constant mass at 70° C, and reweighed. SWC was calculated as

254 the fraction of mass lost during drying (water mass) divided by the leaf dry mass.

255 **Twig diameter at 40 cm from the apex** was measured over bark on three to nine

256 individuals of each species by averaging two perpendicular measurements of leader branches

257 40 cm back from the shoot tip. A significant correlation between twig diameter and shoot

258 extension indicates that the 'shape' of shoots is an important factor influencing growth.

259

260 Irradiance

261 The irradiance environment was characterized above every plant for which extension and

262 diameter growth was measured. One hemispherical photo was taken immediately above the

263 center of each canopy using a self-leveling Nikon Coolpix 4500 camera with a Nikon FC-E8

264 fisheye converter. Hemispherical photos were taken concurrently with the final growth

265 measurements. The captured images were processed using Gap Light Analyzer (Frazer,

266 Canham & Lertzman 1999) to estimate the total fraction of short-wave radiation transmitted

267 through the canopy directly over each measured plant during the course of a year, given

268 latitude and azimuth, hereafter expressed as 'irradiance' (MJ m^{-2} d^{-1}).

269

270 Statistical analyses

271 Bivariate correlations between growth and the 11 traits described above were first examined

272 to identify key traits linked with growth. Partial correlations were then used to better

273 understand the covariation structure among traits and to further identify which traits were

274 associated with growth after partialling out the influence of the other traits. The 'pcor.test'

275 function in the ppcor package for R was used for this analysis (Kim 2015). Exploratory

276 factor analysis was subsequently used to reduce the number of trait dimensions and to

277 identify key axes of variation among traits that were also aligned with growth. The 'esem'

278 function in the psych package for R was used for this analysis (Revelle 2016).

279   Maximum attainable height of a species was the only trait that explained significant

280 ($\alpha = 0.05$) variation in growth after partialling out the influence of the other traits.

281 Furthermore, exploratory factor analysis revealed the clear separation of traits into three axes

282 of variation – traits relating to hydraulic functioning, traits relating to mechanical safety, and

283 traits relating to leaf economics. Informed from these results, structural equation models

284 (SEM) were developed (described below) and tested using the 'sem' function in the lavaan

285 package for R (Rosseel 2012). Structural equation modeling considers both measured and

286 'latent' variables. Latent variables are linear representations of groups of strongly correlated

287 traits (i.e., the 'hydraulic', 'biomechanic', or the 'LES' factors). As such, each latent variable

288 includes the variation in common among two or more measured traits, similar to scores on an

289 obliquely rotated factor, and are presumed to represent a higher-order level of plant

290 functioning, e.g., the hydrologic or biomechanic strategy of the species. Although it was

291 clear from the exploratory factor analysis that three groups of strongly correlated traits (i.e.,

292 latent variables) emerged from the dataset, it was not known if all latent variables would be

293 needed to predict variation in growth. Therefore, SEM was used to test if one, two, or all

294 three of the latent variables (hydraulic, biomechanic, and LES trait groups) were necessary to

295 accurately model growth. SEM was also used to test the direct effect of height on growth, as

296 well as its influence via the measured and latent variables.

297   There are different opinions on how to best evaluate structural equation models. In

298 this case we report the root mean square error of approximation (RMSEa), AIC, chi-sqr p

299 value, and the comparative fit index. Better fitting models exhibit lower RMSEa, whereas

300 lower AIC values may reflect better fit and/or greater regularization. Counterintuitively,

301 better fitting SEM models generally have lower chi-square values and higher associated p

302 values than poorer fitting models. This is because the SEM null hypothesis assumes no

303 difference between the observed data and the proposed model. Therefore, poorly specified

304 SEM models are less congruent with the observed covariance matrix (i.e., higher chi-square

305 values) than appropriately specified models. The comparative fit index (CFI) compares the

306 fit of a specified model to a model where the variables are assumed to be uncorrelated. As

307 such, CFI represents the difference in chi-square between the observed and predicted

308 covariance matrices, with values closer to one indicating better fit. We point readers to Kline

309 (2012) for discussion of the limitations and assumptions of SEM, as well as Belluau &

310 Shipley (2017) (2017) and Grace (2008) for practical application of this method.

311   The first SEM model tested the direct influence of height on growth vs the indirect

312 influence of height on growth, as manifested through the *measured* traits. For example, it is

313 well-understood that plant size may influence volumetric and mass growth rate directly (Hunt

314 1978). However, it is also plausible that height (and access to direct radiation) is coordinated

315 with other traits via natural selection (e.g., xylem-specific conductivity), and that growth is

316 the outcome of these other coordinated traits, rather than height per se. The second model

317 was the same as the first except that the indirect influence of height on growth was allowed

318 only through each of the hydraulic, biomechanic, and LES latent variables. This makes sense

319 if the evolution of height has been coordinated with the hydraulic or biomechanical strategies

320 of species more generally, rather than with individual traits. The third and fourth models

321 tested if all three latent variables were necessary, or if model fit improved meaningfully when

322 some were removed. Model 3 included only the 'hydraulic' latent variable, whereas model 4

323 included both 'hydraulic' and "biomechanic' latent variables.

324   Finally, we wanted to know if differences in irradiance and/or site (tropical,

325 subtropical, temperate) significantly influenced the fitted slope and intercept coefficients of

326   the bivariate analyses. We used the base functions 'aov' and 'TukeyHSD' in R to fit slopes

327   and assess mean separation among the sites, respectively (R Core Team 2015).

328

329   **Results**

330   Trait correlations

331   Species growth rates, measured as length extension or diameter increment of the most

332   vigorous shoots on each plant, were correlated with a range of traits that included the

333   maximum attainable height of the species, leaf size, leaf area per xylem cross-section, xylem-

334   specific conductivity and twig diameter at 40 cm from the tip (Table 1). Although length and

335   diameter increments could in principle give different signals – for example, if some species

336   or individual shoots had more side-branching than others – they proved closely correlated (R^2

337   = 0.81) across the species examined here. Both measures of growth were similarly correlated

338   with most of the traits examined, with the exception that only diameter growth was correlated

339   with wood density and modulus of elasticity (Table 1). Only maximum height was

340   significantly correlated with growth rates after partialling for all other traits (Table 2).

341   Further, only LMA and twig diameter remained significantly correlated with growth after

342   partialling for maximum height (p close to 0.05 in both cases) (Table S2).

343   Exploratory factor analysis revealed clear separation of traits into hydraulic,

344   biomechanic, and LES traits (Table S3), as well as close association of height with the

345   hydraulic trait factor (Table S3). Considering SEM models 1 and 2, model 2 provided a

346   better fit, with the root mean square error of the approximation (RMSEa) decreasing from

347   0.194 to 0.032, and the AIC value decreasing from 958 to 906 (Table 3). This suggests that

348   the latent variables were able to adequately represent the relevant variation in the measured

349   traits, with the predictive capacity of both models for length and diameter growth being only

350   moderately reduced in model 2 (Table 3). This reflects the large degree of multicollinearity

15

351   among the measured traits and supports the hypothesis that the measured traits align with a

352   higher-order axis of variation reflecting plant strategy, and that plant height is the dominant

353   trait associated with this axis. Evaluation of models 2, 3, and 4, revealed that the model

354   including only the hydraulic latent variable (model 3) generally outperformed models

355   including two or all three latent variables, with lower AIC and RMSEa values (Table 3).

356   This suggests that plant traits aligned with the hydraulic factor are able to adequately predict

357   variation in growth (extension and diameter growth $R^2 = 0.43$ and 0.61), without considering

358   biomechanic or LES traits (Table 3). However, because the model including all three latent

359   variables (model 2) provides a much better representation of how hydraulic, biomechanic,

360   and LES traits relate to one another, as well as to height and growth, we have redrawn model

361   2 here (Fig 1). Standardized SEM coefficients represent the change in one variable relative

362   to the change in another (in units of SD) whilst holding the influence of all other relevant

363   variables constant. Although all the hydraulic traits exhibited strong correlation with growth

364   by themselves (Table 1) this influence disappeared almost completely in the SEM because

365   the predictive capacity of these variables was also aligned with the predictive capacity of

366   height on growth. Thus, the 'indirect' effect of height through the latent variables was

367   markedly weak, whereas the 'direct' effect of height on growth was strong (Fig. 1). For

368   example, the coefficients between height and the hydraulic axis were 0.85, whereas the

369   coefficients between the hydraulic axis and growth were weaker (-0.02, 0.25). This does not

370   suggest that the latent variables are not correlated with growth, but that their contributions to

371   growth were also closely aligned with variation in height.

372

373   Site effects

374   Species growth rates measured either as length or diameter increase were greatest at the

375   tropical site (log transformed length growth $F_{2,41} = 21.11$, $p < 0.0001$; log transformed

376   diameter growth $F_{2,41}$ = 18.23, p < 0.0001). Mean length growth across species at each site

377   varied from 7.83 mm y^{-1} (SD = 4.19) at the warm temperate site, to 10.1 mm y^{-1} (SD = 6.51)

378   at the cool temperate site, to 36.2 mm y^{-1} (SD = 18.1) at the tropical site. Similarly, mean

379   diameter growth across species at each site varied from 1.00 mm y^{-1} (SD = 0.67) at the warm

380   temperate site, to 1.14 mm y^{-1} (SD = 0.83) at the cool temperate site, to 4.53 mm y^{-1} (SD =

381   2.43) at the tropical site. Several of the traits that correlated with growth rate also varied with

382   latitude. Nevertheless, maximum height and most of the other traits significantly correlated

383   with growth (Table 1) remained significant after site had been accounted for (see Table S5).

384   In general, traits had a consistent relationship with growth across the sites; interaction terms

385   were rarely significant (see Table S5). Site effects explained between 47% and 52% of the

386   variance in growth rates, and a combination of plant functional traits explained up to an

387   additional 30%. After accounting for site, maximum height explained 17% of the variance in

388   length increase and 30% of the variance in diameter increase – a greater proportion than any

389   other trait (Fig. 2, Table 4).

390   The question arises whether the observed correlation between growth rates and height

391   was due to coordination between growth and maximum-height strategies, or simply as a

392   response to taller plants benefiting from a more favorable irradiance environment. Species

393   tended to be exposed to different irradiance environments both because of differences in

394   irradiance between latitudes, and because of differences in canopy position within sites.

395   However, there was no strong relationship between growth and irradiance either within or

396   among sites in all cases (Fig. 3; R^2 < 0.42 and p > 0.01). Although irradiance did have some

397   predictive capacity (linear models, Table 4), maximum height remained significant even after

398   irradiance was included in the model, and explained 2 to 3 times as much of the variation in

399   length and diameter growth rates (Table 4).

400

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_{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.

18

426   The size of individual leaves was also found to be an important trait correlated with

427   growth and maximal plant height. In part, this may have been because species with larger

428   leaves tend to deploy them more efficiently on the shoot (Pickup, Westoby & Basden 2005;

429   Wright *et al.* 2006) and to experience less within-shoot self-shading (Falster & Westoby

430   2003a). Leaf size has also been found to correlate with 'leafiness' and twig size (Ackerly &

431   Donoghue 1998; Falster & Westoby 2003a; Westoby & Wright 2003; Kleiman & Aarssen

432   2007), which are related via 'Corner's rules' (White 1983). As a consequence of their wider

433   dimensions, however, larger leaves should have a tendency to overheat more than small

434   leaves, assuming the components of energy balance are similar (Monteith & Unsworth 1990).

435   To compensate for this, larger leaves may require a greater investment in transpirational

436   capacity (i.e., a greater capacity for evaporative cooling). We might therefore expect xylem-

437   specific conductivity to be linked with leaf size, as well as leaf area to xylem area ratio, to

438   supply this additional transpiration. To the extent that xylem-specific conductivity may

439   reflect transpirational capacity, our results support this hypothesis.

440   A number of studies have found a positive relationship between maximum height and

441   RGR in forests (Sterck & Bongers 2001; Poorter *et al.* 2008; Martínez-Vilalta *et al.* 2010;

442   Wright *et al.* 2010; Iida *et al.* 2014). Wright et al. (2010) observed that maximum height was

443   part of a suite of traits, including wood density and leaf mass per area, that correlated with the

444   relative growth rate of tropical tree species. Our study is unique in that it not only

445   emphasises the importance of growth-height relationships across a much broader range of

446   species and environments, but also suggests an evolutionary alignment of height and growth

447   with water transport and leaf deployment traits. Although data reported here and elsewhere

448   support correlation between height and growth, the mechanisms underpinning this correlation

449   are not clear. Taller plants might have higher rates of growth for physiological reasons.

450   Taller species are likely to sit higher in the canopy profile and intercept more PAR (Sterck &

451   Bongers 2001; King 2003; Poorter *et al.* 2008). Conversely, height might be expected to

452   have a negative effect on carbon budget via increased xylem and bark (including phloem)

453   maintenance costs (Givnish 1988; Falster & Westoby 2003b). Other ecological benefits of

454   being tall, such as escaping fire (Higgins, Bond & Trollope 2000; Bond, Cook & Williams

455   2012) and browsing (Allcock & Hik 2004), are only gained once a height threshold has been

456   reached, suggesting that the drivers for these benefits may select for both fast growth and tall

457   stature.

458   Greater height may also be a detriment to forest species. Taller plants must transport

459   water farther and higher than other species, resulting in increasing water tension in leaf and

460   twig xylem, and possibly, higher incidence of embolism, and lower rates of stomatal

461   conductance and photosynthesis (Ryan *et al.* 2000; Schäfer, Oren & Tenhunen 2000; Koch *et*

462   *al.* 2004; Domec *et al.* 2008). Mortality rates have not been found to correlate with

463   maximum height in most cases (Wright et al. 2010, Poorter et al 2008), but they may if

464   mechanical safety also declines with height (Iida *et al.* 2014). It has also been reported that

465   traits conferring fast growth may result in higher rates of damage from arthropods (i.e.

466   growth rate hypothesis, Stamp 2003) and may also result in increased susceptibility to

467   damage from falling or wind-driven debris (Clark & Clark 1991; Gleason *et al.* 2008).

468   Conversely, small statured species may grow more slowly because they invest in defense and

469   seed production, therefore benefiting from lower mortality and higher fecundity (Wenk &

470   Falster 2015).

471   In summary, shoot growth across the species and climates examined in this study was

472   correlated with a suite of traits, including maximum height, xylem-specific conductivity, leaf

473   area to xylem area ratio, leaf size, wood density, stem stiffness, and access to PAR, but with

474   the important caveat that maximum height accounted for a significant amount of variation in

475   growth that was independent of variation in the other traits. Taken together, height and

476 growth appear to be closely aligned via natural selection with the hydraulic and

477 biomechanical functioning of wood and leaves. This result also suggests that natural

478 selection has resulted in the near-complete confounding of the independent influence of

479 xylem, leaf, and allometric traits on growth. Considering the marked collinearity among

480 height and growth traits, it will be difficult to dissect the independent influences of traits on

481 growth. Species that do not exhibit marked correlation among height and growth traits, i.e.,

482 species with large residuals from our fitted models, may represent opportunities to better

483 understand why correlation among these traits exists, and under what circumstances this

484 correlation might weaken. Genetically modified genotypes (e.g., "knockouts") might also

485 facilitate the investigation of growth~trait relationships independent of height and other

486 closely allied traits.

487

488 **Authors' Contributions**

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

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491

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500

Data Accessibility

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

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Supporting Information

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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 ($\triangle$), and Cool temperate ($\bigcirc$).

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

28

each species during the course of a year. Sites are denoted by the following symbols: Tropical (+), Warm temperate ($\triangle$), and Cool temperate ($\bigcirc$).

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_{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.

	Length growth (log)	Diam growth (log)	Max height (log)	Leaf-area / xylem-area (log)	Xylem-specific cond. (log)	Leaf area (log)	Wood density	Amax	Leaf N (log)	MOE	LMA (log)	leaf SWC (log)	Stem (twig) diam	Irrad
Number of species measured	44	44	44	36	35	44	44	37	36	38	44	38	44	41
Length growth (log)		**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.073	0.924	0.403	0.273	0.451	0.256	**0.012**	0.120
Diam growth (log)	**0.904**		**< 0.001**	**0.000**	**< 0.001**	**< 0.001**	**0.005**	0.313	0.820	**0.038**	0.707	0.356	**0.000**	**0.049**
Max height (log)	**0.704**	**0.816**		**< 0.001**	**< 0.001**	**< 0.001**	**0.002018**	**0.045**	0.445	0.081	0.405	0.920	**0.001**	**0.019**
Leaf-area / xylem-area (log)	**0.466**	**0.587**	**0.676**		**< 0.001**	**0.011**	0.556	0.230	0.121	0.244	0.948	0.922	0.136	**0.031**
Xylem-specific cond. (log)	**0.566**	**0.724**	**0.794**	**0.730**		**< 0.001**	**0.036**	**0.009**	0.531	0.055	0.071	0.241	**0.006**	**0.001**
Leaf area (log)	**0.530**	**0.659**	**0.740**	**0.420**	**0.776**		**0.003**	**0.039**	0.773	**0.008**	0.123	0.399	**0.000**	**0.010**
Wood density	-0.273	**-0.412**	**-0.453**	-0.102	**-0.355**	**-0.441**		0.042	0.383	**< 0.001**	0.601	0.169	**0.000**	0.746
Amax	0.016	0.170	**0.332**	0.208	**0.436**	**0.341**	**-0.336**		0.376	0.356	**0.020**	0.796	0.114	**0.008**
Leaf N (log)	0.144	0.039	0.131	0.263	0.111	-0.050	0.150	-0.154		0.734	**< 0.001**	**0.016**	0.349	**0.007**
MOE	-0.182	**-0.338**	-0.287	-0.199	-0.327	**-0.423**	**0.600**	-0.156	0.059		0.952	0.451	**< 0.001**	0.455
LMA (log)	-0.116	0.058	0.129	0.011	0.309	0.236	-0.081	**0.382**	**-0.628**	-0.010		**0.019**	0.228	**0.005**
leaf SWC (log)	0.189	0.154	0.017	0.017	0.204	0.141	-0.228	0.044	**0.400**	-0.126	**-0.378**		0.786	0.637
Stem (twig) diameter	**0.375**	**0.547**	**0.487**	0.253	**0.455**	**0.539**	**-0.538**	0.265	-0.161	**-0.623**	0.186	0.046		0.053
Irrad	0.247	**0.309**	**0.366**	**0.376**	**0.554**	**0.397**	-0.052	**0.445**	**-0.458**	-0.131	**0.432**	-0.083	0.304	

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.

	Max height (log)	Leaf-area / xylem-area (log)	Xylem-specific cond. (log)	Leaf area (log)	Wood density	Amax	Leaf N (log)	MOE	LMA (log)	leaf SWC (log)	Stem (twig) diameter
Diameter growth											
r	**0.475**	0.052	0.210	-0.144	0.120	-0.272	-0.172	-0.064	0.039	0.204	0.239
p-value	0.012	0.807	0.314	0.494	0.572	0.185	0.412	0.762	0.855	0.328	0.249
Length growth											
r	**0.565**	-0.171	0.219	-0.240	0.281	-0.280	-0.203	-0.025	-0.147	0.267	0.199
p-value	0.001	0.417	0.293	0.247	0.170	0.172	0.330	0.909	0.486	0.193	0.340

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 R^2) 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).

Length growth

Model number	p (chi-square)	CFI	RMSEa	RMSEa upper CL	RMSEa lower CL	Growth r^2	AIC
1	< 0.001	0.654	0.233	0.288	0.179	0.652	950
2	0.210	0.963	0.073	0.147	< 0.001	0.484	891
3	0.897	1.000	< 0.001	0.127	< 0.001	0.433	376
4	0.610	1.000	< 0.001	0.141	< 0.001	0.442	628

Diameter growth

Model number	p (chi-square)	CFI	RMSEa	RMSEa upper CL	RMSEa lower CL	Growth r^2	AIC
1	< 0.001	0.670	0.233	0.288	0.179	0.684	938
2	0.312	0.981	0.054	0.136	< 0.001	0.639	876
3	0.932	1.000	< 0.001	0.080	< 0.001	0.614	361
4	0.707	1.000	< 0.001	0.125	< 0.001	0.638	611

Table 4. Linear models predicting growth (length and diameter) from irradiance followed by maximum species height. R^2 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.

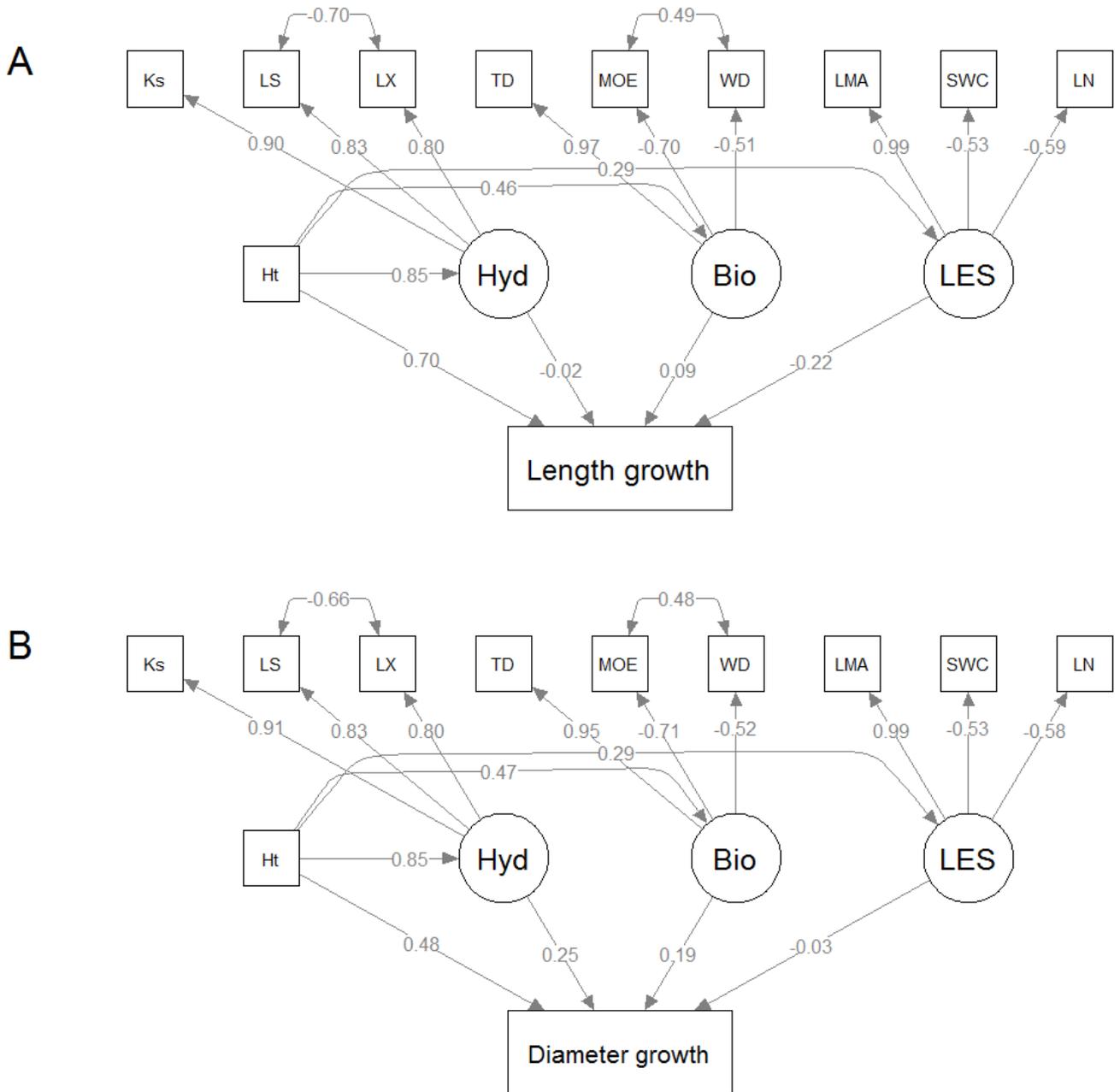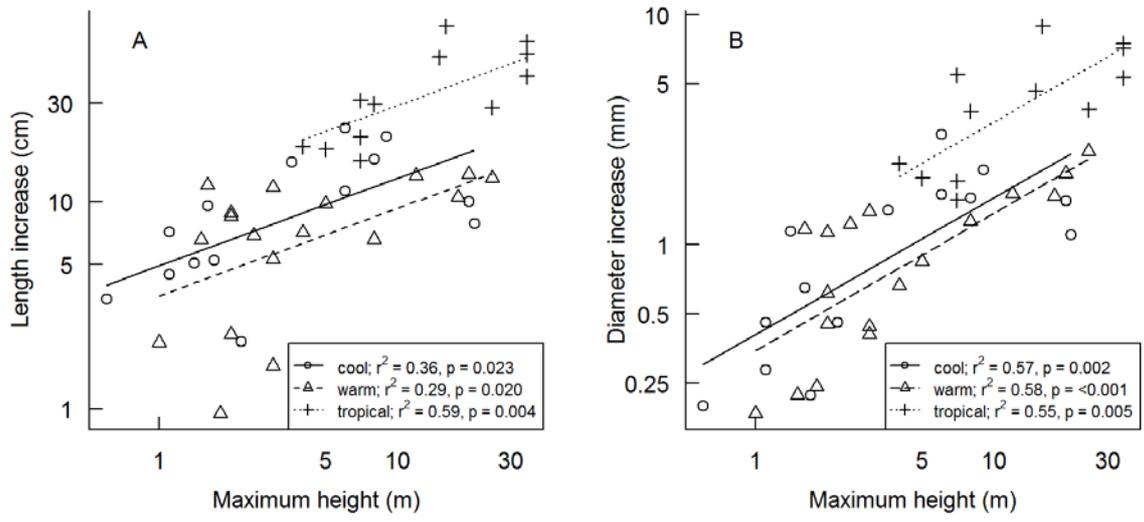|	DF	SS	MS	F	p	Variable R^2
Length growth (log) ~ Irradiance × Maximum height (log)						
Irradiance	1	0.86	0.86	9.38	0.0045	0.14
Maximum height (log)	1	2.51	2.51	27.52	< 0.0001	0.40
Irradiance × Maximum height (log)	1	0.06	0.06	0.65	0.4268	0.01
Residuals	31	2.83	0.09			
Diameter growth (log) ~ Irradiance × Maximum height (log)						
Irradiance	1	1.52	1.52	21.54	< 0.0001	0.23
Maximum height (log)	1	2.98	2.98	42.33	< 0.0001	0.45
Irradiance × Maximum height (log)	1	0.00	0.00	0.04	0.8481	0.00
Residuals	31	2.18	0.07			

Fig. 1

Fig. 2

Fig. 3