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Branch height rather than diameter at breast height drives intraspecific leaf trait variation in large trees of a subtropical evergreen broad-leaved forest

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Abstract

For woody plants, intraspecific trait variation (ITV) serves as a core adaptive strategy to resist hydraulic failure and physical damage. However, how ITV varies with branch height and diameter at breast height (DBH) remains relatively underexplored compared with interspecific trait variation. To investigate ITV across different branch heights and DBH, we selected 14 large individuals of *Castanopsis chinensis* in an old-growth subtropical evergreen broad-leaved forest in southern China. We collected branch samples from the bottom to the top of each tree and measured seven functional traits related to leaf carbon gain, hydraulics, and mechanical strength, including leaf size (LS), leaf non-structural carbon concentration (NSC), leaf area to sapwood area ratio (A_L/A_S), leaf petiole length (LPL), leaf folding angle (LFA), leaf punching strength (F_p) and leaf mass per area (LMA). Our results showed substantial ITV in plant traits, with A_L/A_S exhibiting the greatest variation and LFA the least. LS, A_L/A_S and LFA decreased significantly with branch height, whereas NSC and LPL increased significantly with branch height. Additionally, both F_p and LMA exhibited significantly positive correlations with branch height, with the strongest associations observed across all measured functional traits. However, none of the traits were significantly correlated with DBH. Our study demonstrates substantial trait variation within a single species and highlights branch height, rather than DBH, as the primary driver of this ITV. These findings reveal distinct differences in carbon allocation,

water use, and physical damage resistance across branch heights, which are vital for plants to cope with external stresses at different vertical branch layers.

Keywords

Functional traits, intraspecific trait variation, leaf area to sapwood area ratio, mechanical strength, non-structural carbon concentration, tree size

Introduction

Intraspecific trait variation (ITV) refers to trait differences among individuals within a species or population, and it is driven by both genetic factors and phenotypic plasticity (Siefert et al., 2015; Pritzkow et al., 2020; Westerband et al., 2021). It enables trees to adjust resource allocation to maintain carbon uptake and reduce the risk of hydraulic failure for survival under climate change (Rosas et al., 2019; Smith-Martin et al., 2026). Therefore, ITV is key to understanding how individual trees use resources throughout their lifespan (Schuldt et al., 2016; Liang et al., 2019).

Changes in branch height and DBH significantly affect ITV (Bin et al., 2022; Spennati et al., 2026). There are two main mechanisms explaining how ITV changes with branch height (Fig. 1).

One is light and water driving mechanism. With increasing branch height, vertical solar radiation in the canopy increases sharply (Matsuo et al., 2022). Meanwhile, long water transport distance and high gravitational potential cause a drop in water potential at the upper canopy, with high risk of xylem embolism (Liu et al., 2018; Fang et al., 2021). In response, the values of both LS and A_L/A_S are usually low at the canopy top for reduced transpiration water loss and accelerated heat dissipation (Leigh et al., 2017; Towers et al., 2024). LFA also decreases with branch height, and upper leaves tend to be more vertical while lower leaves are more horizontal (Hollinger, 1989). Vertical upper leaves reduce excessive light absorption and let light reach the lower canopy for high whole-plant carbon accumulation (Long et al., 2006).

The other mechanism is outside physical damage driving mechanism. In particular, increasing branch height raises the risk of physical damage and herbivory, such as wind damage and insect browsing (McCormick et al., 2012; Bennett et al., 2015). A large exposed canopy area at great height makes upper branches more vulnerable to wind (Gardiner et al., 2008; Iida et al., 2012). Strong winds take away water and heat from the surface of the leaves (He et al., 2025). Therefore, high branches usually have a small LS, high LMA, and thick cuticles. Long and flexible petioles are also an adaptation to reduce wind resistance (Filartiga et al., 2022). Additionally, large trees are more vulnerable to herbivore browsing (Fernández-de-Uña et al., 2023), due to their high visual noticeability and large surfaces for releasing volatile organic compounds (McCormick et al., 2012; Castagneyrol et al., 2013; Thon

et al., 2024; Volf et al., 2026). To defend herbivory, trees invest more carbon in leaf structural tissues for improved leaf mechanical strength (Lusk et al., 2010; He et al., 2019).

Although it is known that tree ITV changes significantly with increasing branch height and DBH (Hietz et al., 2017; Maynard et al., 2022; Yang et al., 2023; Carle et al., 2026), it remains debated which factor is the core mechanism driving this variation, due to high collinearity between the two variables during natural tree growth (Fu et al., 2017). Therefore, we randomly selected 14 mature *Castanopsis chinensis* trees (45 cm ≤ DBH ≤ 121 cm) from an old-growth subtropical evergreen broad-leaved forest in southern China. Branch samples were collected from the bottom to the top, across a height range of 2 m to 21 m. Seven functional traits closely related to plant hydraulics, carbon allocation, and physical resistance were measured (Table 1). We propose the following two chief hypotheses:

Hypothesis 1: As branch height and DBH increase, LS, LFA, and A_L/A_S will decrease, while NSC reserves will increase. Trees are expected to reduce LS and LFA to minimize water consumption through leaf transpiration induced by high light with increasing branch (Koch et al., 2004; Wright et al., 2017; Bittencourt et al., 2026). Meanwhile, trees increase leaf NSC reserves to mitigate potential leaf damage caused by high light and water deficit at forest canopy layers (McDowell & Allen, 2015; Li et al., 2026).

Hypothesis 2: As branch height and DBH increase, LPL, LMA, and F_P will increase as well. This structural adaptation is a key strategy for trees to withstand mechanical disturbances (e.g., wind and rain) and insect browsing (Castagneyrol et al., 2013; He et al., 2025).

Materials and Methods

Study site

The study area is located in the Dinghushan National Nature Reserve, Guangdong Province (112°30′39″–112°33′41″E, 23°09′21″–23°11′30″N). This is a typically subtropical evergreen broad-leaved primary forest, estimated to be over 400 years old (Huang et al., 2016), with *Castanopsis chinensis* as the dominant species. Because *C. chinensis* is the tallest tree species in this forest, it is vulnerable to climate change, such as global warming and seasonal droughts. This has led to an increasing number of dead trees in recent decades (Zhou et al., 2013; He et al., 2022). We randomly selected 14 large individuals of this tree (45 cm ≤ DBH ≤ 121 cm). For each tree, we collected sun-exposed branches from the bottom to the top (Figs. S1 and S2), resulting in a total of 63 samples.

Leaf morphological traits

LS (cm^2) was scanned with a scanner (CanoScan LiDE 120) and calculated in ImageJ software (National Institutes of Health, Bethesda, MD, USA). LPL (mm) was measured via a vernier caliper. LFA (°) refers to how much the leaf margin curls relative to the main vein in the leaf cross-section. Leaf cross-sections were cut and fixed in their natural folded state, and cross-section images were taken using a scanner, with the angles then measured via ImageJ.

Plant A_L/A_S and leaf NSC

The cut branches were wrapped in wet wipes and taken to the laboratory as soon as possible. After bark removal, the diameters of the branches and piths were measured with a vernier caliper to calculate the sapwood area. Because the collected branches were between 8 mm and 1 cm in diameter and were all 1 to 2 years old, there was no heartwood in them (Fig. S4). Therefore, the sapwood area was calculated by subtracting the bark and pith diameters from the stem diameter. A_L/A_S ($cm^2\ cm^{-2}$) is the ratio of leaf area to sapwood cross-sectional area.

NSC ($mg\ g^{-1}$) was calculated as the sum of soluble sugars and starch, which were sequentially extracted based on their distinct solubilities, and both fractions were quantified using the anthrone-sulfuric acid method. After sampling, tissues were immediately put into an oven, heated at 105 °C for 30 min to stop enzyme activity, and then dried at 65 °C until constant weight. Dried samples were ground into fine

144 powder and sieved. We weighed 0.2 g of powder into a 15 mL centrifuge tube, mixed
145 with 6-7 mL of 80% ethanol, and kept in an 80 °C water bath for 30 min for
146 extraction. The mixture was centrifuged at 3000 rpm for 5 min, with the upper liquid
147 kept. The remaining solid was extracted again twice (10 min each time), and the upper
148 liquid was collected after each centrifugation, mixed together and evaporated in an
149 85 °C water bath to 2-3 mL. The liquid was moved to a 50 mL volumetric flask, and
150 distilled water was added to volume. Anthrone ethyl acetate reagent and concentrated
151 sulfuric acid were added for color reaction. Absorbance was measured at 630 nm with
152 a spectrophotometer, and soluble sugar content was calculated using a sucrose
153 standard curve.

154 The solid left after soluble sugar extraction was used to measure starch. Distilled
155 water (3 mL) was added to the solid, then the mixture was heated in boiling water for
156 15 min for gelatinization. After cooling, 2 mL of cold 9.2 mol L^{-1} perchloric acid was
157 added and stirred occasionally. The mixture was extracted for 15 min, distilled water
158 was added to make the total volume 10 mL. After 10 min of centrifugation, the upper
159 liquid was moved to a 50 mL volumetric flask. The solid was extracted again with
160 another 2 mL cold 9.2 mol L^{-1} perchloric acid for 15 min with stirring, and distilled
161 water was added to 10 mL. After centrifugation, the upper liquid was collected, and
162 the solid was washed 1-2 times with distilled water. All collected upper liquids were
163 put into the same 50 mL volumetric flask, and distilled water was added to volume.
164 Color reaction was carried out using the anthrone-sulfuric acid method with blank

samples. Absorbance was measured at 620 nm, and starch content was calculated using a starch standard curve (Wang et al., 2018).

Leaf mechanical properties

F_P (kN m^{-1}) is the maximum force per fracture circumference along the leaf lamina surface (Onoda et al., 2011). This parameter was measured via a puncture test with a digital force gauge (precision 0.001N, HADPI-20, Leqing, China). The maximum force required for a 0.6-mm-diameter probe to penetrate the leaf was recorded, and the average values were calculated. LMA (g cm^{-2}) is the ratio of leaf dry weight which was excluded the petiole to leaf area.

Statistical analyses

Simple linear regression was performed using the "lm" function in R software (version 4.5.1) to explore the relationships between functional traits and tree size. Pearson correlation analysis was used to calculate correlation coefficients (r) and explanatory power (R^2), with statistical significance set at $P < 0.05$.

Principal component analysis (PCA) was conducted using IBM SPSS Statistics 27.0.1 to evaluate trait associations and variance axes. Trait correlations and their contributions to the principal components were assessed based on their positions and angles.

A path model was constructed to evaluate the direct and indirect effects of branch height on functional traits. The Chi-square test was used as the primary criterion for model validity: when χ^2 was small and $P > 0.05$, there was insufficient evidence to reject the model. Path coefficients were used to measure the strength of the effects, with larger absolute values indicating stronger effects. Solid lines generally represented significant path coefficients, and dashed lines represented non-significant ones.

Results

Trait Variation within Species

This study quantified the magnitude of ITV and revealed significant variability in most traits. Among leaf morphological traits, LS showed the largest variation, varying by about 7.6-fold. This was followed by LPL, which increased from 4.68 mm to 25.67 mm (about a 5.49-fold change). LFA showed the smallest variation, varying by about 1.8-fold (Table 1). For plant hydraulic efficiency, A_L/A_S showed the largest variation, changing by about 17.9-fold. In contrast, the variation in NSC was relatively small, at about 2.6-fold. Regarding leaf mechanical properties, both F_P and LMA varied by nearly 3-fold (3.06-fold and 2.98-fold, respectively).

Correlation of Functional Traits with Branch Height and DBH

205 The study determined that DBH was not significantly correlated with any of the
206 measured functional traits (all $P > 0.05$; Figs. 2-4). In contrast, branch height was the
207 main factor driving the measured functional traits, as all traits were significantly
208 correlated with branch height (all $P < 0.05$). Among leaf morphological traits, LS,
209 LFA, and LPL were significantly correlated with height, with R^2 values ranging from
210 0.202 to 0.5 (positive correlation: LPL; negative correlations: LS, LFA; Fig. 2b, d, f).
211 Additionally, A_L/A_S was significantly negatively correlated with branch height (R^2 =
212 0.345, $P < 0.001$; Fig. 3b). NSC significantly increased with branch height (R^2 =
213 0.148, $P = 0.002$; Fig. 3d). Regarding mechanical strength, both F_P ($R^2 = 0.660$, $P <$
214 0.001; Fig. 4b) and LMA ($R^2 = 0.644$, $P < 0.001$; Fig. 4d) were significantly
215 positively correlated with branch height.

216

217 *PCA*

218 PCA was used to evaluate the associations among plant functional traits, branch
219 height, and DBH. The first principal component axis (PC1) explained 53.43% of the
220 variation in the variables, while the second axis (PC2) explained 13.65% of the
221 variation. The positive end of PC1 was associated with branch height, F_P, LMA, LPL,
222 and NSC, whereas the negative end of PC1 was associated with LS, A_L/A_S, and LFA.
223 DBH was distributed along the second axis, indicating a decoupled relationship
224 between DBH and the other traits (Fig. 5).

Path models

To directly quantify the regulatory mechanisms of branch height on plant functional traits, we used path modeling to analyze the relationships among the variables. Model (a) showed that branch height directly drove the variation in LS and LMA. Specifically, branch height had a strong positive effect on LMA and a negative effect on LS. The increase in LS, in turn, had a negative impact on LMA. Furthermore, the decrease in LMA subsequently led to a significant increase in A_L/A_S, indicating an indirect regulation of A_L/A_S via LS (Fig. 6a). In Model (b), branch height directly influenced the changes in F_P and LMA, showing strong driving effects (Fig. 6b). LMA then directly affected F_P and A_L/A_S. Specifically, a higher LMA led to a significant increase in F_P and a significant decrease in A_L/A_S.

Discussion

By measuring seven functional traits related to leaf morphology, plant hydraulics, and physical resistance, we investigated the ITV of 14 *Castanopsis chinensis* individuals with branch height and DBH. Contrary to some previous studies (Rüger et al., 2012; Yin et al., 2023; Umaña et al., 2025), we found that DBH did not significantly affect ITV. Instead, the measured functional traits were highly and significantly correlated with branch height (with F_P and LMA showing the strongest correlations).

Changes in LS, LFA, A_L/A_S, and NSC with branch height and DBH

Our first hypothesis proposed that as branch height and DBH increased, LS, LFA, and A_L/A_S would decrease, while NSC reserves would increase. Our results partially supported this hypothesis and demonstrated significant associations between plant traits and branch height, yet the associations between plant traits and DBH were not confirmed. Hydraulic limitation hypothesis (HLH) suggested that with increasing branch height, leaf water potential became more negative due to long hydraulic transport paths and high gravitational potential, whereas our own findings showed that leaf water potential did not significantly decrease with branch height (Fig. S3). One recent study on Dipterocarpaceae, the world's tallest angiosperm family and a dominant group in Southeast Asian rainforests, also reported a similar trend (Bittencourt et al., 2026). That study attributed this pattern to full compensation for height-related hydraulic limitation via vessel widening and a reduced hydraulic threshold. Therefore, water deficit did not drive the variation in plant traits especially for hydraulic traits. Meanwhile, we found that photosynthetically active radiation (PAR) increased significantly with branch height ($R^2 = 0.878$, $P < 0.001$; Fig. S3). Temperature followed a similar trend, with a moderate positive relationship to branch height ($R^2 = 0.478$, $P = 0.027$; Fig. S3). Therefore, we speculated that light exposure at high branch height drove the variation in leaf traits. Our previous studies also showed that light is the main limiting factor for plant growth and survival in this old-

growth subtropical evergreen forest (He et al., 2019, 2022). The reduction in LS and LFA at high branches could lower transpiration-driven water loss, increase heat dissipation, and prevent photoinhibition (Falster & Westoby, 2003; Wright et al., 2017).

There are two possible interpretations for NSC accumulation with increasing branch height. One is that sufficient light in the canopy enables leaves to produce more organic compounds and accumulate greater amounts of NSC (Huang et al., 2024; Shao et al., 2024). The other reason is that high NSC concentrations allow canopy leaves to repair damage induced by high light, high temperature and water deficit more rapidly, which is an effective protective strategy for the leaves at canopy layers (He et al., 2020; Moore et al., 2021; Xiao et al., 2024)

LPL, LMA, and F_P with respect to branch height and DBH

Our second hypothesis was also partially supported by our results. As branch height increased, LPL, LMA, and F_P increased. However, unlike branch height, none of these three traits showed a significant correlation with DBH. The increase in LMA and F_P reflected a response to the greater risk of physical damage such as wind and rain resulting from increasing branch height (Iida et al., 2012; Takagi et al., 2018), and this reinforcement in leaves allowed plants to effectively resist tearing and washing by strong winds and rains (Enrico et al., 2016). In addition, this

reinforcement allowed leaves to avoid herbivore browsing. This was mainly because high LMA usually indicated leaves with high tissue density, thick mesophyll, a large proportion of cell walls and abundant fibres (Lusk et al., 2010; Gianoli et al., 2024), while F_P acted as a physical barrier that hindered browsing by herbivores (Kitajima et al., 2012; Salgado-Luarte et al., 2023; Gianoli et al., 2024). Furthermore, the final explanation was that high LMA and leaf mechanical strength were usually associated with thick leaves, which contained more mesophyll cells per unit leaf area and thus could more efficiently utilize high-intensity light for photosynthetic carbon fixation (Peguero-Pina et al., 2017; Mizokami et al., 2022). Finally, we also found that LPL increased with branch height. This was because long and flexible petioles improved the leaves' ability to reconfigure their shape in dynamic wind fields to reduce drag (Filartiga et al., 2022).

DBH does not affect plant traits of large trees

Our study revealed that DBH non-significantly correlated with any of plant traits of this large tree (Tables S1 and S2). These findings differ from previous studies, which concluded that DBH significantly affects traits such as LS and LMA (Rüger et al., 2012; Yin et al., 2023; Umaña et al., 2025). To explain this discrepancy, we speculate that the effects of DBH on plant traits observed in previous studies might be an indirect correlation resulting from its use as a proxy for branch height. In those studies, DBH was likely used as the sole measure of tree size, thereby confounding

the driving effects on functional traits that should have been attributed to branch height. By independently evaluating the effects of branch height and DBH on plant traits, our study showed that the variation in plant traits at least ITV was driven by branch height rather than DBH. Therefore, DBH may not show independent statistical significance when both branch height and DBH are considered simultaneously.

Conclusion

This study revealed that branch height, rather than DBH, is the primary driver of variation in plant functional traits. External environmental changes such as light and temperature caused by increasing branch height might drive the shifts in plant traits. These shifts with branch height are critical to plant carbon acquisition, water use and physical defense. However, under global climate change, these height-driven adaptive strategies may face new challenges such as die-back in the old and large trees if carbon starvation and/or hydraulic failure occur in the tree crown (McDowell et al., 2008; McDowell & Allen, 2015). Therefore, future research should integrate both internal effects (e.g., branch height) and external effects (e.g., changing climate) to evaluate the vulnerability of tall trees.

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Author contributions

P.H. and Y.W. conceived the idea. P.H., H.L., Y.N., G.W., W.W., Q.H., Q.L., M.L., X.L., R.J., Q.N., C.G. and L.L. carried out plant functional trait measurements. Y.W. and P.H. analyzed the data. Y.W., P. H. and X.T. wrote the initial manuscript. All authors contributed substantially to subsequent versions.

Data availability statement

The data that support the findings of this study are archived in Zenodo: https://doi.org/10.5281/zenodo.18874417. DOI: 10.5281/zenodo.18874417.

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537 Zhou, G., Peng, C., Li, Y., Liu, S., Zhang, Q., Tang, X., ... & Chu, G. (2013). A
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540 *Biology*, *19*(4), 1197-1210.

541 **Table 1** Variables used in this study.

Symbol	Trait	Unit	Min.	Max.	Mean	CV
DBH	Diameter at breast height	cm	44.60	121.00	68.24	0.34
Height	Branch height	m	2.00	21.30	11.45	0.47
LS	Leaf size	cm^2	6.97	53.10	25.84	0.40
LPL	Leaf petiole length	mm	4.68	25.67	13.92	0.34
LFA	Leaf folding angle	^{o}	100.00	180.00	148.94	0.11
A_L/A_S	Leaf area to sapwood area ratio	$cm^2\ cm^{-2}$	615.47	11035.04	5967.77	0.40
NSC	Non-structural carbon content	$mg\ g^{-1}$	93.31	242.83	150.98	0.20
F_p	Leaf punching force	$kN\ m^{-1}$	0.33	1.01	0.64	0.27
LMA	Leaf mass per area	$g\ cm^{-2}$	61.66	184.01	115.12	0.27

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Figure legends

Figure 1 Conceptual diagram of functional traits influenced by branch height and environmental stress. Through combined effects of hydraulic disruption and biotic attack, trees achieve a dynamic trade-off and optimization of resource uptake and allocation (carbon and water) by adjusting the pattern of functional traits that vary with branch height.

Figure 2 ITV in leaf morphological traits with branch height and DBH. (a) LS and DBH; (b) LS and Height;(c) LPL and DBH; (d) LPL and Height;(e) LFA and DBH;(f) LFA and Height. Shaded areas indicate confidence intervals. R^2 and P values are reported. Trait abbreviations are the same as in Table 1.

Figure 3 ITV in A_L/A_S and NSC with branch height and DBH. (a) A_L/A_S and DBH;(b) A_L/A_S and Height;(c) NSC and DBH;(d) NSC and Height. Shaded areas indicate confidence intervals. R^2 and P values are reported. Trait abbreviations are the same as in Table 1.

Figure 4 ITV in leaf mechanical properties with branch height and DBH. (a) F_p and DBH; (b) F_p and Height; (c) LMA and DBH; (d) LMA and Height. Shaded areas indicate confidence intervals. R^2 and P values are reported. Trait abbreviations are the same as in Table 1.

Figure 5 Principal component analysis for plant traits for the first two axes. Trait abbreviations are the same as in Table 1.

Figure 6 Path models of relationships among plant traits across 14 individuals. (a) Model exploring the effects of branch height on LS, LMA and A_L/A_S. (b) Model exploring the effects of branch height on F_p, LMA and A_L/A_S. Numbers on arrows are standardized path coefficients. R^2 values at the top-right corner of each variable represent the proportions of variations explained. Dashed arrows indicate nonsignificant paths, whereas solid arrows indicate significant paths. Trait abbreviations are the same as in Table 1.

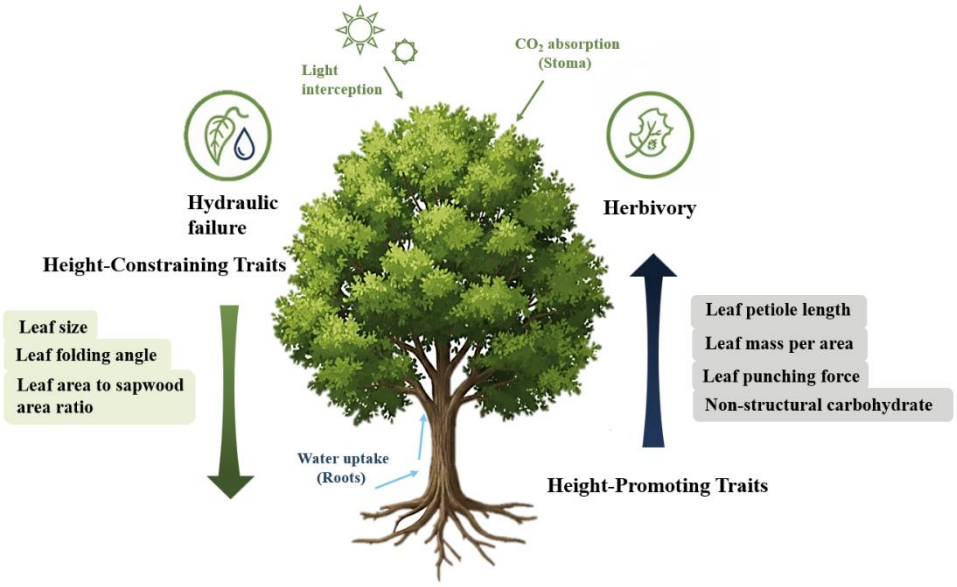
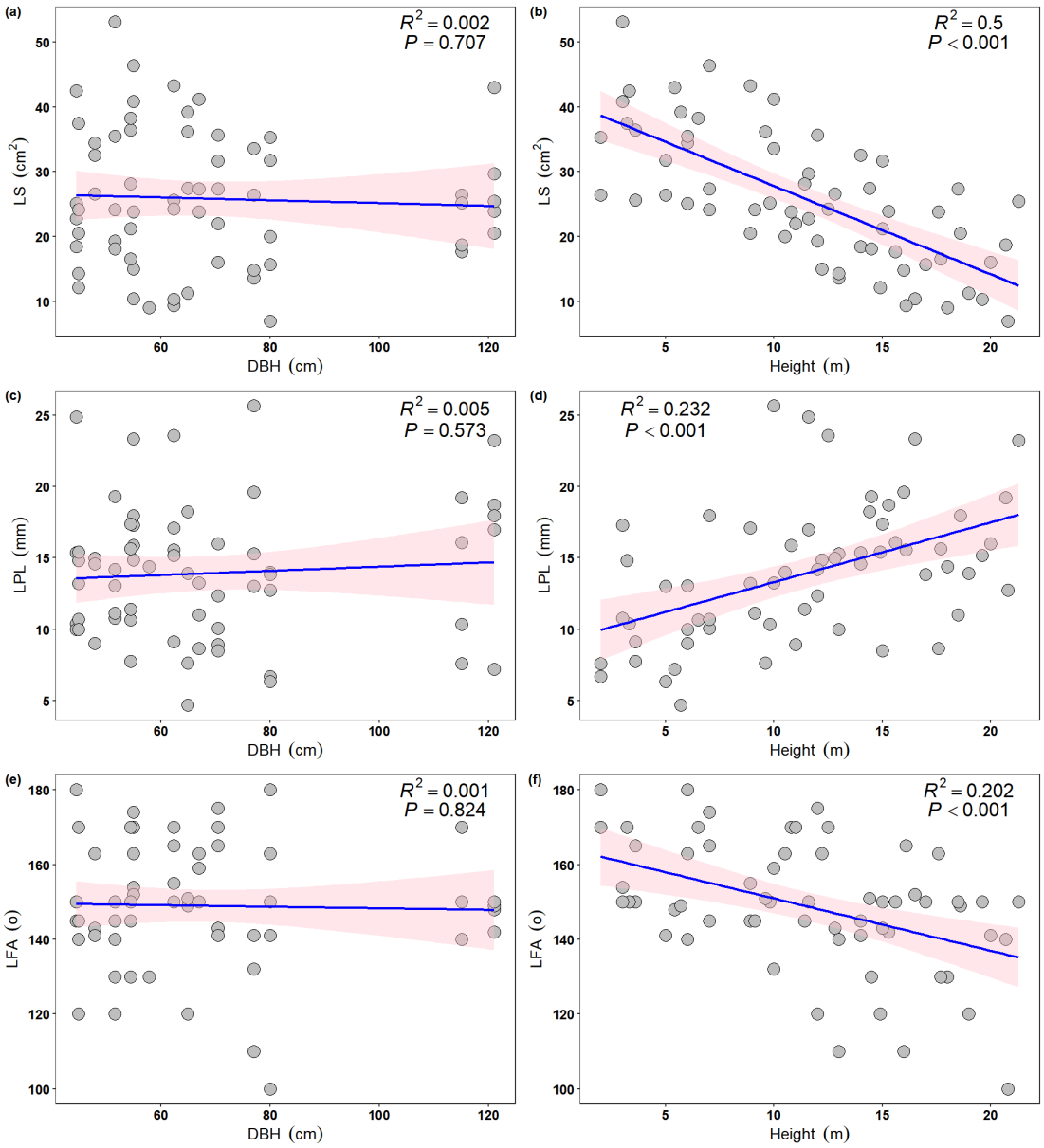
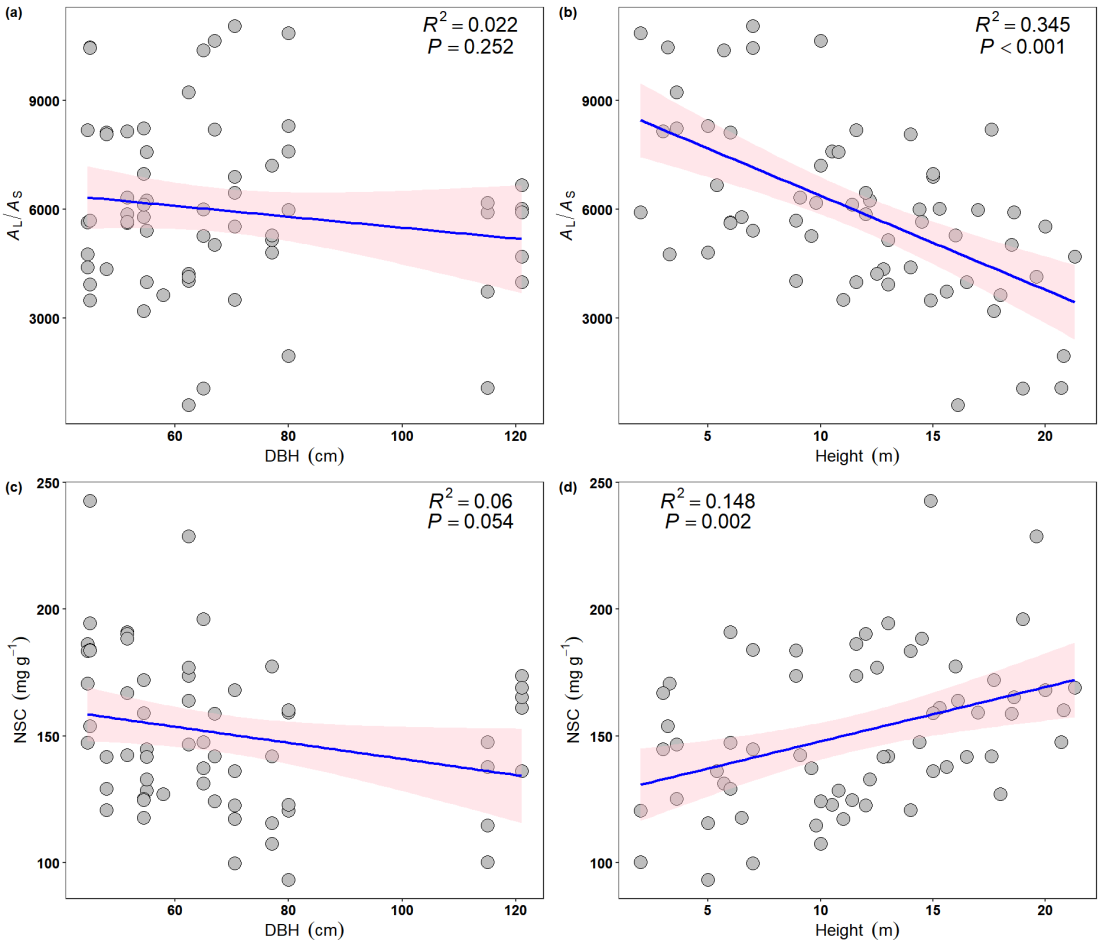

Light interception
CO_2 absorption (Stoma)
Hydraulic failure
Herbivory
Height-Constraining Traits
Leaf size
Leaf folding angle
Leaf area to sapwood area ratio
Leaf petiole length
Leaf mass per area
Leaf punching force
Non-structural carbohydrate
Water uptake (Roots)
Height-Promoting Traits

Figure 1



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576 **Figure 2**



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578 **Figure 3**

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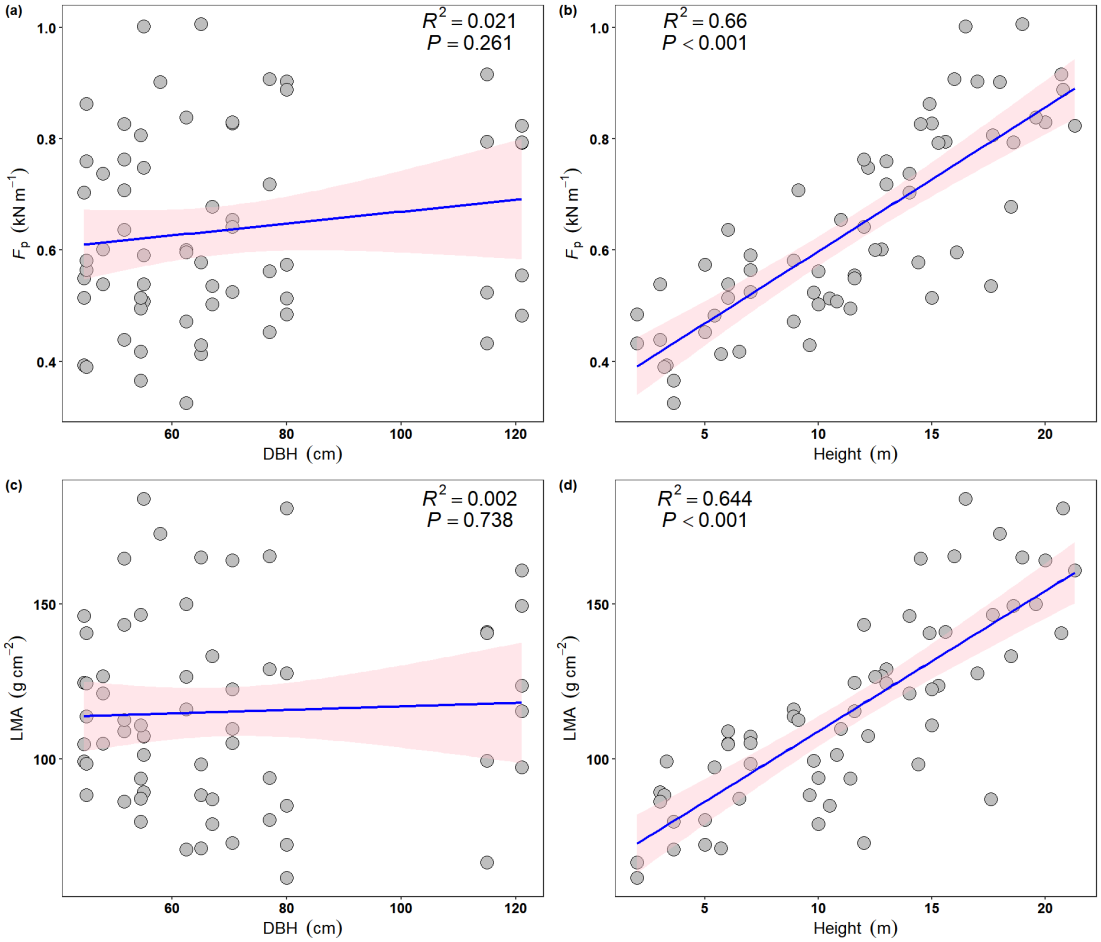
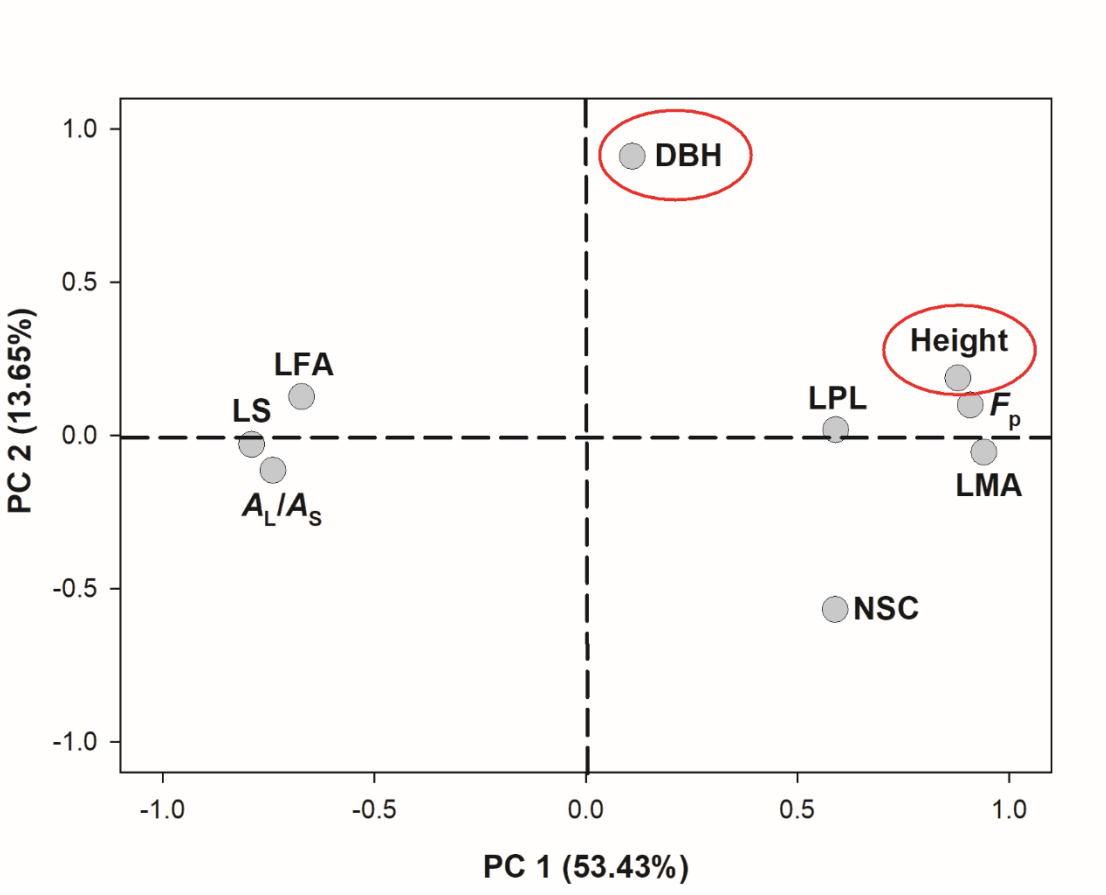

(a)
$R^2 = 0.021$
$P = 0.261$
F_p (kN m^{-1})
DBH (cm)
(b)
$R^2 = 0.66$
$P < 0.001$
F_p (kN m^{-1})
Height (m)
(c)
$R^2 = 0.002$
$P = 0.738$
LMA (g cm^{-2})
DBH (cm)
(d)
$R^2 = 0.644$
$P < 0.001$
LMA (g cm^{-2})
Height (m)

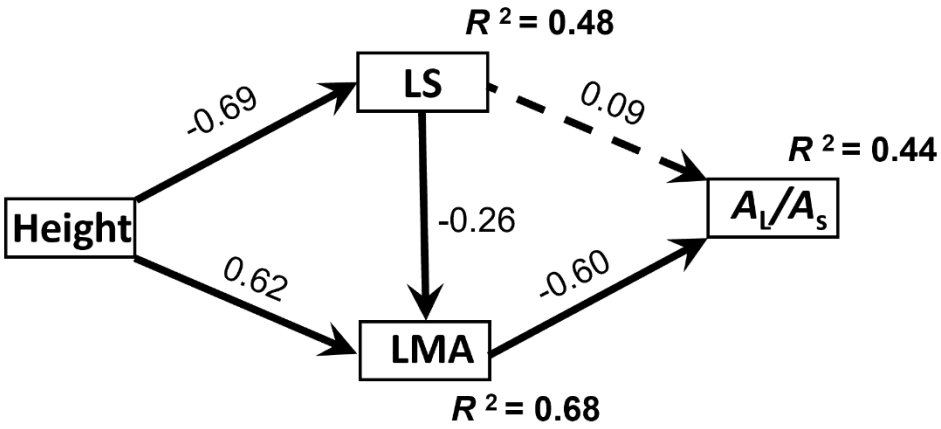
Figure 4



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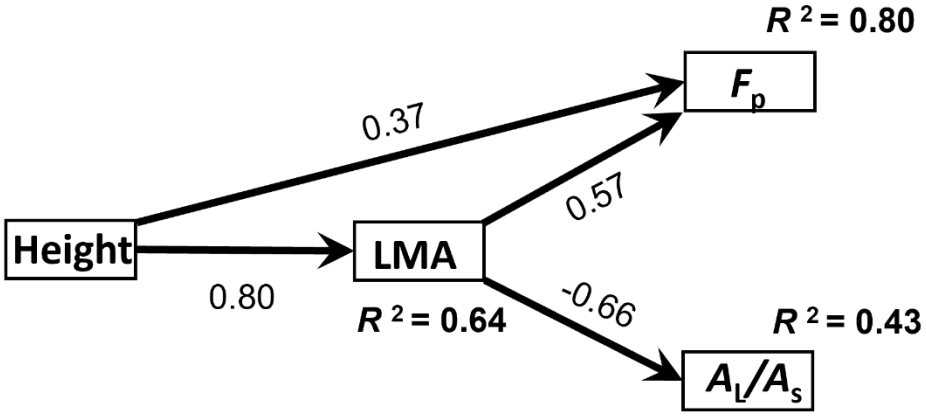
585 **Figure 5**

(a) **Model a:**



$\chi^2 = 0.678$, $df = 1$, $P = 0.410$, AIC = 18.678

(b) **Model b:**



$\chi^2 = 1.044$, $df = 2$, $P = 0.593$, AIC = 17.044

Figure 6

Supplementary Files

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