

Different performing trees manifest varied scaling relationships at individual and branch levels

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Abstract

Competition is an important factor influencing the structure and dynamics of plant communities, and understanding species coexistence. Tree architectural traits, such as height-to-diameter (H-D) and branch length-to-diameter (L-d) relationships influence species competitiveness through affecting light capture by altering the occupation of space. Unfortunately, little is known about how the H-D and L-d scaling allometric exponent related to tree performance (growth vigour) in competition. We surveyed 1739 (1642 living and 97 dead) individual trees from an even-aged dense aerial seeding forest of Masson pine (*Pinus massoniana*), in which 51 trees with 1087 first-order branches were destructively sampled. Using the H-D and branch L-d scaling data, we determined (1) whether the H-D scaling exponent numerically differed across different levels of tree performance, and (2) whether the L-d scaling relationship differed across tree performance and branch vertical position in crowns. The results indicate that (1) the H-D scaling exponent numerically decreased as tree performance deteriorated; (2) the L-d scaling relationship differed across tree performance, and the numerical value of the scaling exponent of “inferior” trees was significantly larger than that of “moderate” and “superior” trees; (3) the L-d scaling exponent declined as branch position approached ground level, and it was significantly higher in upper branches; and (4) overall, the branch scaling exponent numerically decreased as tree vigour ameliorated in each canopy layer, but decreased significantly only in the intermediate layer. This study highlights the variation within (and linkage among) length-to-diameter scaling relationships across tree performance at the individual and branch levels. This linkage provides novel insights into tree competitive strategies and potential mechanisms of tree mortality in the competition of subtropical forests.

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Running title: tree performance relates to scaling allometry

Abstract

Competition is an important factor influencing the structure and dynamics of plant communities, and understanding species coexistence. Tree architectural traits, such as height-to-diameter ($H-D$) and branch length-to-diameter ($L-d$) relationships influence species competitiveness through affecting light capture by altering the occupation of space. Unfortunately, little is known about how the $H-D$ and $L-d$ scaling allometric exponent related to tree performance (growth vigour) in competition. We surveyed 1739 (1642 living and 97 dead) individual trees from an even-aged dense aerial seeding forest of Masson pine (*Pinus massoniana*), in which 51 trees with 1087 first-order branches were destructively sampled. Using the $H-D$ and branch $L-d$ scaling data, we determined (1) whether the $H-D$ scaling exponent numerically differed across different levels of tree performance, and (2) whether the $L-d$ scaling relationship differed across tree performance and branch vertical position in crowns. The results indicate that (1) the $H-D$ scaling exponent numerically decreased as tree performance deteriorated; (2) the $L-d$ scaling relationship differed across tree performance, and the numerical value of the scaling exponent of “inferior” trees was significantly larger than that of “moderate” and “superior” trees; (3) the $L-d$ scaling exponent declined as branch position approached ground level, and it was significantly higher in upper branches; and (4) overall, the branch scaling exponent numerically decreased as tree vigour ameliorated in each canopy layer, but decreased significantly only in the intermediate layer. This study highlights the variation within (and linkage among) length-to-diameter scaling relationships across tree performance at the individual and branch levels. This linkage provides novel insights into tree competitive strategies and potential mechanisms of tree mortality in the competition of subtropical forests.

Keywords: competition, height-diameter, intraspecific variation, mortality, performance, scaling, *Pinus massoniana*

1 Introduction

Competition is a fundamental process affecting the structure and development of plant communities (Tilman 1982; Niklas & Hammond 2013; Iida *et al.* 2016; Rozendaal *et al.* 2020). Individuals are eliminated via inter- and intraspecific interactions, among which conspecific interactions induce intense competitive pressure, especially in the early stages of succession (Martin-Ducup, Schneider & Fournier 2016; Aussenac *et al.* 2019). The competitive advantages of trees involve several factors including the ability to capture soil resources and sunlight (Ford 2014; Kunstler *et al.* 2016), which is often closely related to different functional traits (e.g., wood density and specific leaf area) (Adler *et al.* 2014). Consequently, functional traits have been used to predict and explain tree performance (Poorter *et al.* 2018; Bongers *et al.* 2020), although no key trait related to tree performance has been canonically adduced (Iida *et al.* 2016). However, few studies have focused on the relationship between competitive advantage and tree architecture. As both tree height and branching patterns related to light interception (Kohyama & Takada 2012), crown form, therefore, is an important factor related to tree mortality (Arellano *et al.* 2019). Hence, for deeply understanding tree

competition strategies and mechanisms of tree mortality, it is essential to explore whether differences in tree performance are correlated with morphometric differences in crown architecture.

Multiple traits and metrics pinpoint the ecological process well (Paal, Zobel & Liira 2020). Scaling relationships provide one method to explore the relationship between tree performance and plant architecture using integrated paired architecture characteristics, e.g., the height-to-diameter ($H - D$) scaling relationship (e.g., McMahon 1973; Niklas 1995). Brown *et al* (2004) proposed the metabolic theory of ecology (MTE), which has been widely applied to a broad range of research areas from organelles to ecosystems (Price *et al.* 2012), and, at the individual and population level, yields predictions about the architecture and demography of trees (Price *et al.* 2010; Loubota Panzou *et al.* 2018). Indeed, the tree height-to-diameter ($H - D$) scaling relationship has been applied to describe the strategies both theoretically and empirically (Sumida, Miyaoura & Torii 2013; Zhang *et al.* 2019a). Numerous research showed the $H - D$ scaling allometric exponent varied among and within species (Feldpausch *et al.* 2011; Loubota Panzou *et al.* 2018; Mensah *et al.* 2018; Zhang *et al.* 2019a). Previous studies indicate that trees can alter their architecture and thus their strategy to compete with rivals (Lintunen & Kaitaniemi 2010; Zhang *et al.* 2020). For example, it was widely accepted that plant density (and thus competition) can alter the numerical values of scaling exponents. Lines *et al* (2012) reported that plants with large neighbors are relatively tall for a given diameter. Qiu *et al* (2021) demonstrated the $H - D$ allometry exponent of Ponderosa pine increased as their neighbor competition enhanced (Qiu *et al.* 2021). The variation of $H - D$ allometry in turn influences the competitiveness of trees (Poorter *et al.* 2003; del Río *et al.* 2019), since differences in trunk diameter and crown shape affect spatial occupation and light interception (Osunkoya *et al.* 2007). However, how tree performance (growth vigour) is linked to $H - D$ scaling allometric exponent remains unclear, especially in terms of intraspecific interactions believed to be essential components of community and ecosystem functioning (Bolnick *et al.* 2011; Poorter *et al.* 2018). Thus, an important question is whether the $H - D$ scaling relationship differs as a function of tree performance?

To answer this question, we determined the numerical value of the intraspecific $H - D$ scaling exponent across different levels of tree performance, predicting on theoretical grounds that it would decrease as tree performance deteriorated. In addition, because tree architecture is determined not only by the trunk but also by first-order branches (Kunz *et al.* 2019), we examined tree performance in the context of the interactions among repetitive self-similar modules, in which the first-order branch is the most fundamental (Kozłowski *et al.* 2012; Kramer, Sillett & Carroll 2014; Loehle 2016). We focused on branch traits such as growth in length and diameter, which change along with their relative position in crown depth (Umeki & Seino 2003; Lemay, Pamerleau-Couture & Krause 2019). In light of these phenomena, ecologists have constructed branch diameter and length models across species and different life stages (Bentley *et al.* 2013; Dong, Liu & Bettinger 2016; Kaitaniemi, Lintunen & Sievänen 2020). Additionally, branch traits also respond to competition, and thus alter the tree competition strategy (Lintunen & Kaitaniemi 2010; Wang *et al.* 2018). However, to the best of our knowledge, no report has linked the branch length-diameter ($L - d$) scaling exponent to tree performance (defined in the context of growth vigour).

Therefore, an important second question is whether the branch $L - d$ scaling exponent differs across tree performance and branch position? Plant invest more to crown extension can intercept more horizontal light (Xu *et al.* 2019). We hence hypothesized that the branch $L - d$ scaling exponent of superior trees will be numerically higher than that of inferior trees, and that the branch $L - d$ scaling exponent will decrease as the position of branches within a crown approach ground level.

To specifically address these two questions, we determined the $H - D$ and $L - d$ scaling relationships of conspecific trees across different performance levels (for criteria, see Materials and Methods), and the branch scaling relationships in different canopy layers (upper, intermediate, and lower) in a high-density aerial seeding of a Masson pine (*Pinus massoniana*) forest. This uniform and almost even-age high-density forest provided an ideal living laboratory for an investigation of growth vigour because of the near homogeneity of abiotic environmental factors.

2 Material and methods

2.1 Study area description

The study was conducted in Luoxi Town, Taihe County, Jiangxi Province, China (114.47°41.55"E, 26deg51'14.73"N). This site has a subtropical monsoon humid climate with mean annual precipitation of 1438 mm, mean annual temperature of 18.9 and mean annual relative humid of 79 % (<http://data.envbox.net/>). The soil is red soil developed from a quaternary red clay, characterized with almost no humid layer and full of gravel on the surface due to water erosion. Masson pine, an evergreen coniferous tree, is an important species for timber production in southern China and its rosin is also one of the most important chemical raw materials. In addition, this species has become an excellent pioneer tree species for afforestation of barren hills in China, due to its resistance to drought and barrenness and strong adaptability. Consequently, aerial seeding of Masson pine has been widely established in southern China to limit the intensive soil erosion and accelerate the restoration of forest vegetation (Xiao *et al.* 2015).

2.2 Sampling measurement protocols

Two plots (20 m x 60 m and 20 m x 50 m) were established on a flat forest with the same slope (14deg) and aspect (336deg; 0 to 360deg measured in degrees from north). All trunks with diameters >1 cm at breast height (1.3 m) were tagged and measured for trunk diameter at breast height (D to the nearest 1 mm) through a measuring tape, tree height (H) through a telescopic measuring pole. Meanwhile, the dead trees with tip were also measured. Tree performance was grouped into three classes: "inferior", "moderate", and "superior" using the criteria described by Simard: (1) "moribund", near death, little or no visible shoot growth; (2) "poor," little or possibly etiolated shoot growth, few and/or short needles; (3) "moderate", moderate shoot growth, leaf area, needle length; and (4) "good", vigorous shoot growth, high leaf area, long needles, deep green color (Simard 1993). We merged "moribund" and "poor" into the "inferior" class because these trees have little or no chance for survival. Subsequent measurements of aboveground biomass and growth rates were consistent with visual identifications (Table 1). Biomass and growth rate are commonly used to quantify tree competitiveness, and to further determine tree performance in competition (Zhang *et al.* 2019b; Wang *et al.* 2021). The significant and dramatic decrease in biomass and growth rate as tree performance deteriorated reinforced the premises of our research ($p < .01$, Table 1). Before using the criteria revised from Simard to assess tree performance in plots, a pre-experiment was conducted next to the sample plot, in which 15 trees (5 repetitions x 3 classes) were cut, showing the biomass and growth rate were significant different between performance levels. The tree density in our study plot is 8264 individuals per hectare, when we surveyed in August 2018. Though we acknowledge there are a few indigenous *P. massoniana* before seeding and few recruitments after sowing, most trees are in the same age, 12 yr (determined by the rings from our destructively sampled trees). While few *Toxicodendron succedaneum* and *Rhus chinensis* scattered in this forest and were measured, only *P. massoniana* was analysed due to the negligible number of other species. Statistical analysis was only performed on trees not shorter than 3 m (H [?] 3 m) in this study for the following two reasons, the first was that trees shorter than 3 m were recruitments and evidently younger than other trees, and the second was that trees shorter than 3 m were completely suppressed and had very little influence on the taller trees. With this criterion, a total of 1739 pine trees (1642 living and 97 dead) were used to ascertain how H - D scaling relationship related to tree performance.

Seventeen representative trees were destructively sampled from each tree performance classes ($N = 17$ trees x 3 classes = 51 trees, except for dead trees), for measuring biomass and diameter growth and exploring branch length-diameter (L - d) scaling relationships. For each tree, healthy and mature needles were collected in the four cardinal directions at one quarter, half-way, and three-quarters of the crown spread (Fig 1A). Branch segments (~ 5cm) were collected from representative intact branches in the four cardinal directions acropetally outward from the base to the tip. Three segments were cut from one quarter, half-way, and three-quarters of the total branch length (Fig 1B). A 5 cm thick transverse section was cut at every meter along the length (height) and the breast-height (1.3m) of each trunk (Fig 1C). All samples were placed into sealed plastic bags to prevent the loss of water, and stored in an icebox to prevent decomposition until they were transported to the laboratory.

Branch diameter at 3 cm from the base was measured to record branch diameter (d) for each branch; the

distance from branch base to the apex was measured as length (L). The distance of the base of each branch from the apex of each tree was also measured. The total fresh weight of the trunk, branches, and leaves of each tree was determined using a hanging scale to the nearest 5 g.

The fresh weight of each sample was measured with an electronic balance to the nearest 0.01 g on the day of collection. The dry mass of all samples was obtained after drying samples at 105 °C for 30 min (stem samples for 1 h) and then continued at 65 °C until a constant weight was reached. All dried disks were scanned into bitmap images at a 600 dpi resolution (Epson Perfection V800 Photo scanner) after being polished with 120 mesh sanding paper. The width of rings was measured with WinDENDRO (V.6.1d). The average D increase over three years was used as a proxy for growth rate. Along the crown length, the crown of each tree was divided into three equal vertical layers: upper, intermediate and lower, and the corresponding branches were also classified into these three layers (Coble, Fogel & Parker 2017).

2.3 Statistical analysis

Dry mass content (DMC) of each sample was calculated as:

$$\text{DMC} = \frac{W_{FS} - W_{DS}}{W_{FS}},$$

where W_{FS} and W_{DS} are fresh weight and dry weight, respectively. We multiplied the total fresh weight of each tissue by the corresponding DMC to obtain the dry biomass of every individual tree. A power-law function was used to describe the scaling relationship between trunk D and H or branch diameter (d) and length (L):

$$y = \beta \xi^a,$$

where y represents H or L , x represents D or d , β is the normalization constant, and a is the scaling exponent (Niklas 1994). To stabilize the variance, data were log-transformed as $\log(y) = \log(\beta) + a \log(x)$ (Niklas 1994). Similar to previous statistical analyses (Zhang *et al.* 2016; Sun *et al.* 2019), standard major axis (SMA) regression of the log-transformed data was used to determine the numerical value of scaling exponents (a) and normalization constants (β) (Smith 2009). The heterogeneity of scaling exponent was significantly, when the 95 % confidence intervals did not overlap. One-way analyses of variance (ANOVA) with least significant difference (LSD) fisher multiple comparisons was used to test differences in biomass, growth rates, and leaf mass per branch. In addition, the Benjamini-Hochberg method was used for p -value correction. All statistical analyses were performed using the statistical software environment R (version 3.6.0) (R Core Team 2019); SMA regression was performed using the package *smatr* (version 3.4-8) (Warton *et al.* 2012). All tests for heterogeneity were based on $p < 0.05$.

3 Results

3.1 The trunk H - D scaling exponents among tree performance

The H - D scaling exponent differed numerically as a function of tree performance; it decreased as tree performance deteriorated ($p < .001$; Table 2; Fig 2B). The scaling exponent of superior trees ($a = 0.58$, 95 % CIs = 0.54 - 0.62, $p < .001$) was significantly larger than that of moderate trees ($a = 0.51$, 95 % CIs = 0.49 - 0.53, $p < .001$), inferior trees ($a = 0.49$, 95 % CIs = 0.46 - 0.52, $p < .001$), and dead trees ($a = 0.43$, 95 % CIs = 0.36 - 0.50, $p < .001$). No significant differences in H - D scaling exponent was observed among moderate, inferior, and dead trees ($p > .05$). Pooling all the data for living trees, the H - D scaling exponent ($a = 0.47$, 95 % CIs = 0.46 - 0.48, $p < .001$) was similar to that of the dead and inferior trees, but significantly differed from that of moderate and superior trees (Table 2; Fig 2A).

3.2 The branch L - d scaling exponent among tree performance and branch position

The branch L - d scaling exponent of all individuals was 1.31 (95 % CIs = 1.27 - 1.35, $p < .001$; Table 2; Fig 3A). Likewise, the branch scaling exponent showed significant differences across tree performance ($p < .01$). The L - d scaling exponent significantly decreased from 1.50 (95 % CIs = 1.42 - 1.59, $p < .001$) for inferior trees to 1.33 (95 % CIs = 1.25 - 1.41, $p < .001$) for moderate trees, and 1.34 (95 % CIs = 1.27 -

1.41, $p < .001$) for superior trees (Table 2; Fig 3B). The $L-d$ exponent also numerically decreased as branches deepened within the crown ($p < .001$), i.e., from 1.34 (95 % CIs = 1.25 - 1.44, $p < .001$) for upper branches, to 1.09 (95 % CIs = 1.04 - 1.14, $p < .001$) for intermediate branches, and 1.02 (95 % CIs = 0.97 - 1.08, $p < .001$) for lower branches (Table 2; Fig 4A).

In the intermediate and lower canopy layers, the branch $L-d$ scaling exponent decreased as tree performance deteriorated (Table 2, Fig 4CD). Furthermore, numerical differences in the branch $L-d$ exponent of trees among different growth vigour were significant only in the intermediate canopy layer ($p < .001$, Fig 4BCD). Specifically, the $L-d$ scaling exponent of inferior trees ($a = 1.34$, 95 % CIs = 1.23- 1.46, $p < .001$) was significantly numerically larger than that of moderate trees ($a = 1.08$, 95 % CIs = 0.97- 1.20, $p < .001$) or superior trees ($a = 1.04$, 95 % CIs = 0.98-1.14, $p < .001$) (Table 2; Fig 4C).

4 Discussion

Competition for resources among plants generates stress such that some plants adapt to survive while others gradually die under the stress. To understand the mechanism of plant performance differences under intraspecific competition, we studied the scaling relationships at the individual and branch level from the perspective of canopy structure. The results indicate that with the deterioration of tree growth vigour, intraspecifically tree growth in height with respect to trunk diameter (i.e. the $H-D$ scaling exponent) decreased, while branch growth in length with respect to diameter (i.e., the $L-d$ scaling exponent) increased. This research improved our understanding of canopy architecture and the mechanisms underlying competition-induced tree mortality.

4.1 Differences in the $H-D$ scaling exponents among different growth vigour

Consistent with our first hypothesis, the $H-D$ scaling exponent significantly differs among tree performance (growth vigour) levels. Specifically, the exponent numerically decreases as tree growth vigour deteriorated (Fig 2B, Table 2). The numerical similarity between the scaling exponents of living and dead trees is attributable to the significant variation in the scaling exponents observed for living individuals (Fig 2A, Table 2). The significantly higher scaling exponent of superior trees indicates that superior trees grow taller with respect to diameter increments. The statistically insignificant difference in the scaling exponents of dead trees and inferior trees is consistent with the observation that inferior trees are likely to die very soon.

The study indicate that in addition to competition (Trouve *et al.* 2015; Qiu *et al.* 2021), climate (Hulshof, Swenson & Weiser 2015; Fortin *et al.* 2018), forest structure (Feldpausch *et al.* 2011), and species composition (Mensah *et al.* 2018), the numerical values of the $H-D$ scaling exponent differ as a function of tree performance (growth vigour) within species. In addition, our results did not support the 2/3-scaling (elastic self-similarity) “law” between tree height and trunk diameter at the intraspecific level coinciding with previous research (Russo, Wiser & Coomes 2007; Mensah *et al.* 2018).

It has been shown that competition stimulate vertical growth of tree (Wright *et al.* 2004; Sun *et al.* 2019), and the growth in height of suppressed trees exceeds that of their dominant counterparts with equivalent diameters (Sumida, Miyaura & Torii 2013; Trouve *et al.* 2015), which appears to contradict the results reported here. This inconsistency may be attributed to the fact that the trees in our study were aerially sowed such that the trees examined are almost even-aged. Consequently, the disparities in tree height are insufficient to have provided an obvious advantage. In communities composed of uneven-aged trees, young trees established under the shade of taller trees typically grow rapidly in height compared to their growth in girth resulting in large slenderness ratios (i.e., H/D) even at the expense of reducing the ability to resist bending forces (Henry & Aarssen 1999). Plant height is a crucial component of light interception (Wright *et al.* 2004; Liu *et al.* 2019), and trees are known to adopt a growth strategy favoring growth to height to establish their canopies in ways that maximize light interception (Banin *et al.* 2012; Hulshof, Swenson & Weiser 2015). The plasticity of the slenderness ratio reflects the ability of trees to self-adjust their growth responses to stressful environments (Bourque, Bayat & Zhang 2019). In general, cadres of individual trees with numerically large height vs. trunk diameter scaling exponents manifest a competitive advantage over trees that grow more slowly in height (Ford 2014).

4.3 Change of branch scaling relationship across growth levels and layers

Contrary to one of our hypotheses, the scaling exponent governing the relationship between branch length vs. diameter of inferior trees numerically exceeded that of superior or moderate trees, which indicates that inferior trees appear to invest more growth in branch length compared to girth (Fig 3B, Table 2). This phenomenology may confer an advantage with regard to canopy spread and light interception (Newton *et al.* 2012; MacFarlane & Kane 2017; Van de Peer *et al.* 2017). Longer branches (i.e., wider crown) allow plants to capture more light resource (Iida *et al.* 2014; Loubota Panzou *et al.* 2018). However, in our study, individual trees that tended to increase branch length compared to growth in thickness also tended to fall into the inferior category of tree performance. One possible explanation for the trends observed in our study is that the leaf biomass per branch of inferior trees is significantly smaller compared to trees assigned to the other categories of tree performance (Fig 5). The total tree leaf area is a decisive factor in the utilization of light energy (Shiet *al.* 2015), and the leaf area is proportional to leaf biomass. Thicker branches provide greater mechanical rigidity and thus tend to carry more leaves, which has long been summarized by Corner’s Rule (Corner 1949). A recent study demonstrated that the stem diameter limits leaf biomass at the twig level (Sun *et al.* 2019), and the sum of the cross-sections of twigs is the same as that of the first-order branch (Chiba 1998), which supports our results at the branch level. Another possible reason for the variation in the scaling of branch length vs. thickness is the “compensatory effect”, i.e., inferior trees extend their branches allowing leaves to be illuminated sufficiently to compensate for their lack of leaves. Our study has shown that different strategies at the individual level are adopted by trees to cope with light competitors. At the individual level, trees with greater height have a competitive advantage for light, while at the branch level, a strategy of increasing branch thickness to sustain the mechanical loads of more photosynthetic organs improves energy acquisition and transformation. These results are in line with the trade-off between tree height gain and crown expansion (Osunkoya *et al.* 2007).

Another of our hypotheses was confirmed, i.e., the branch length vs. diameter ($L - d$) scaling exponent decreases as the location of branches deepens within the crown and differs across tree performance in the intermediate layer. The variant $L-d$ scaling exponent among branches in different canopy layers indicates that the scaling of branches depends on location and perhaps age (because branches closer to the ground level tend to be branches produced during the earlier growth of trees).

Previous studies indicate that branch traits such as diameter, length, and death vary as a function of the relative position of branches within a canopy (Umeki & Seino 2003; Chen & Sumida 2017; Lemay, Pamerleau-Couture & Krause 2019). Our study highlights the co-variance of branch traits along crown-depth based on scaling relationships. The competition for light and space maybe the main driver of this pattern. The space within a canopy tends to become more and more crowded basipetally from the top to the bottom of a crown such that the horizontal growth of upper branches is not as limited for space. Thus, the scaling exponent for the branches in the upper part of the canopy tends to be numerically larger than that for branches lower within the canopy. Interestingly, branches in intermediate layer tend to intercept more light than those of upper and lower branches because the upper branches are illuminated fully but hold low biomass (hence less leaf) whereas the bottom branches are light deprived because of shelf-shading within the canopy (Osada & Takeda 2003). Consequently, the fiercest competition for light and space within canopies tends to be in the intermediate layer, which leads to a significant difference of branch $L - d$ scaling exponent in this layer among tree performance levels. Meanwhile, this research can provide references for pruning in management. In pruning, branch diameter rather than length should be considered preferentially, and more attention should be paid to the branches in intermediate layer.

Finally, it is worth noting that the statistically significant dissimilarities in the scaling exponents among tree conspecifics assigned to different growth vigour draws focus on the importance of intraspecific variance (Bolnick *et al.* 2011). The scaling exponent of inferior and moderate trees significantly differs from that of superior trees at the individual level, indicating that, in addition to studying trees growing under optimal growth conditions (Poorter *et al.* 2018), averaging all the data drawn from all the individuals within a study site can bias and obscure our understanding of community scaling relationships.

5 Conclusion

Overall, we proved that in Masson pine forests, tree performance relates to architectural traits. We found tree performance relates to the scaling exponent at both individual and branch levels, that is trees with a higher H - D scaling exponent grow better, whereas trees with lower branch L - d scaling exponent perform better in competition. In addition to the decrease of L - d scaling exponent as the position of branches deepens within crown, we also found that the linkage between L - d scaling exponent and tree performance is determined by the intermediate branches. The linkage between scaling exponent and tree performance improves our understanding of tree competitive strategies and mechanisms of tree mortality. This research also highlights that the interspecific variation of morphological traits should not be ignored. More species should be considered in future research.

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Conflicts of Interest: The authors declare no competing financial interests.

Data Accessibility Statement: data used in the analysis will be available through Dryad until acceptance of this manuscript.

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- Table 1** Aboveground biomass and mean growth rate (mean \pm se, n = 17) of trees of different growth vigor. Different lowercase denotes significant differences at the 0.05 level.

Growth vigor	Above-ground biomass (g)	Growth rate (mm yr ⁻¹)
inferior	2482.51 \pm 158.43 c	4.51 \pm 0.36 c
moderate	4466.34 \pm 242.91 b	6.35 \pm 0.30 b
superior	6727.18 \pm 284.23 a	8.03 \pm 0.38 a

	Group	n	α (95 % CI)	β (95 % CI)	R^2	p
<i>H</i> vs. <i>D</i>	dead	93	0.425(0.360, 0.502)	0.419(0.393, 0.445)	0.382	<0.001
	inferior	465	0.491(0.463, 0.520)	0.419(0.405, 0.432)	0.600	<0.001
	moderate	704	0.507(0.485, 0.529)	0.389(0.374, 0.404)	0.658	<0.001
	superior	293	0.579(0.543, 0.618)	0.290(0.258, 0.322)	0.687	<0.001
	living	1462	0.469(0.456, 0.482)	0.412(0.403, 0.420)	0.714	<0.001
<i>L</i> vs. <i>d</i>	inferior	332	1.502(1.421, 1.589)	0.059(0.040, 0.078)	0.737	<0.001
	moderate	421	1.330(1.245, 1.420)	-0.017(-0.030, -0.003)	0.637	<0.001
	superior	334	1.340(1.273, 1.411)	-0.050(-0.062, -0.037)	0.713	<0.001
	upper	251	1.343(1.249, 1.444)	-0.099(-0.119, -0.079)	0.672	<0.001
	inferior in upper	76	1.587(1.388, 1.814)	-0.001(-0.063, -0.614)	0.669	<0.001
	moderate in upper	76	1.309(1.137, 1.507)	-0.110(-0.136, -0.084)	0.659	<0.001
	superior in upper	99	1.355(1.174, 1.566)	-0.120 (-0.149, -0.091)	0.485	<0.001
	intermediate	392	1.088(1.037, 1.141)	-0.019(-0.030, -0.009)	0.738	<0.001
	inferior in intermediate	113	1.341(1.229, 1.463)	0.046(0.018, 0.073)	0.726	<0.001
	moderate in intermediate	126	1.076(0.967, 1.197)	-0.013 (-0.033, 0.006)	0.625	<0.001
	superior in intermediate	153	1.037(0.948, 1.135)	-0.039(-0.056, -0.022)	0.653	<0.001
	lower	444	1.022(0.970, 1.076)	0.063 (0.053, 0.072)	0.725	<0.001
	inferior in lower	143	1.101(0.982, 1.234)	0.084(0.064, 0.105)	0.633	<0.001
	moderate in lower	132	1.095(0.987, 1.215)	0.053(0.036, 0.069)	0.658	<0.001
	superior in lower	169	0.995(0.921, 1.074)	0.056(0.041, 0.071)	0.774	<0.001
All branches	1087	1.312(1.272, 1.354)	-0.014 (-0.022, -0.006)	0.726	<0.001	

Table 2 Summary of reduced major axis (RMA) regression results (slopes and y -intercepts, β and α , respectively) for trunk height (H) versus diameter (D) among growth vigour levels (dead, inferior, moderate and superior), and for branch length (L) versus diameter (d) across growth vigour and the vertical relative position in the crown (upper, intermediate and lower)

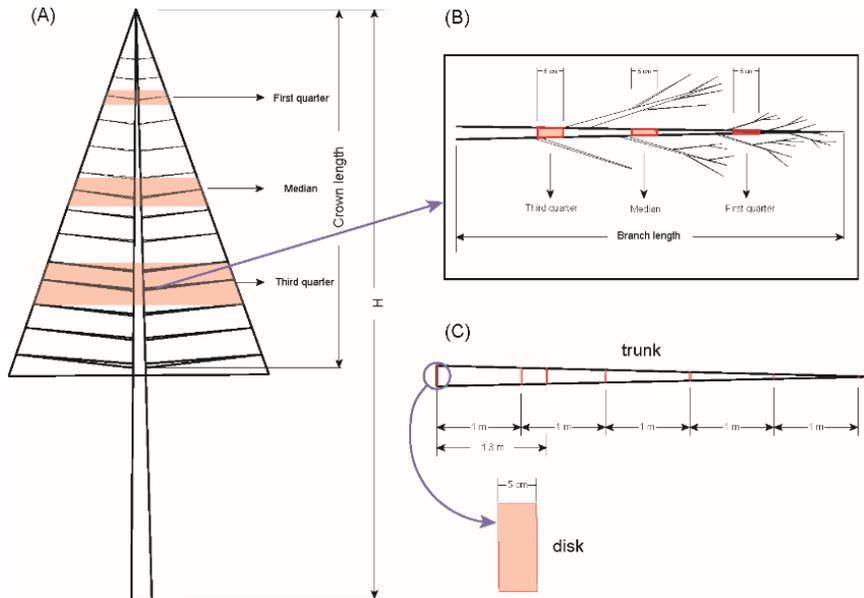


Figure1 The schematic diagram of sampling position leaf and branch position (A), of branch sampling (B), and stem sampling (C).

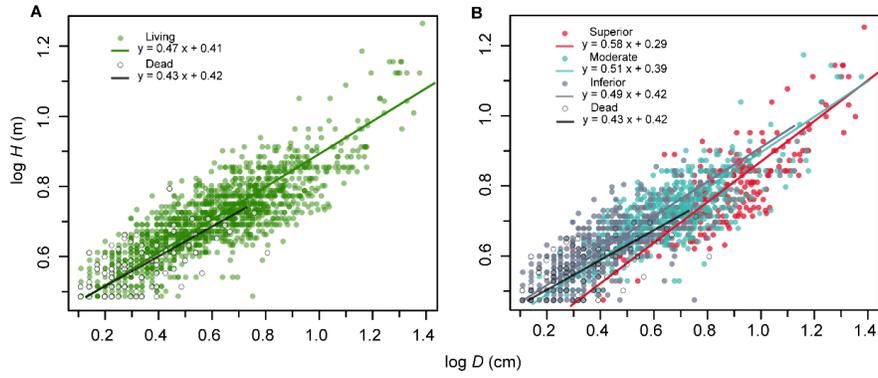


Figure 2 Relationships of tree height (H) and diameter at breast height (D) for the pooled data (living and dead) (A), and for plants grouped by growth vigour levels (superior, moderate, inferior and dead) (B). Statistical parameters for standard major axis (SMA) regressions are shown in Table 2.

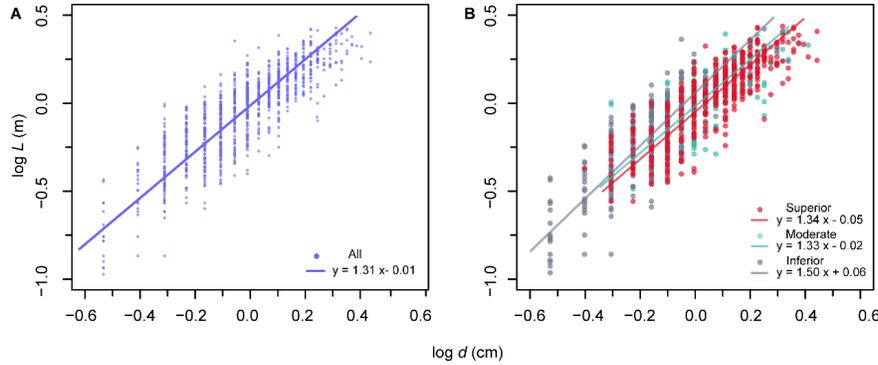


Figure 3 Relationships of branch length (L) and diameter (d) for the pooled data (living and dead) (A), and for plants grouped by growth vigour levels (superior, moderate, inferior and dead) (B). Statistical parameters for standard major axis (SMA) regressions are shown in Table 2.

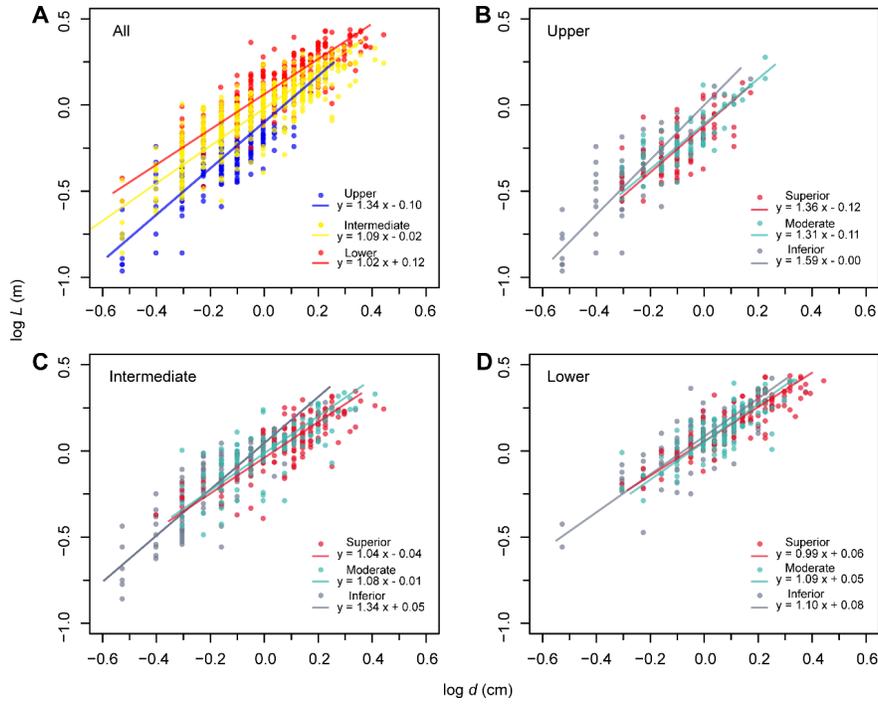


Figure 4 Relationships of branch length (L) and diameter (d) grouped by the relative vertical position in the crown (upper, intermediate and lower) (A); relationships of L and T in the upper layer branches grouped by growth vigour levels (superior, moderate, inferior) (B), in the intermediate layer grouped by vigour (C), in the lower layer grouped by vigour (D). Statistical parameters for standard major axis (SMA) regressions are shown in Table 2.

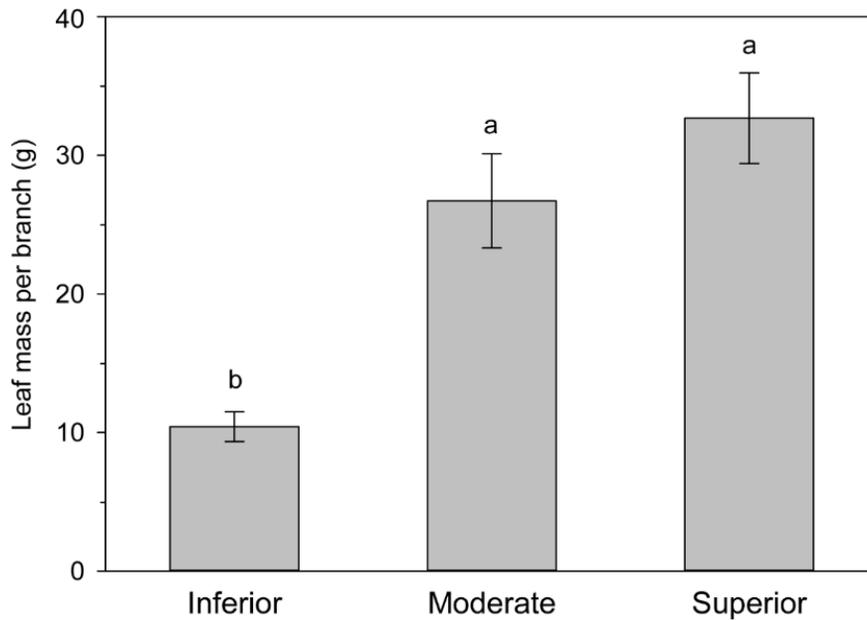


Figure 5 The leaf mass per branch among growth vigour. The error bars indicate standard errors. Different lowercase letters denote significant differences at the 0.05 level.

