


RESEARCH ARTICLE

Competitive performance of *Pinus massoniana* is related to scaling relationships at the individual plant and branch levels

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Abstract

Premise: Competition is an important driver of tree mortality and thus affects forest structure and dynamics. Tree architectural traits, such as height-to-diameter (H - D) and branch length-to-diameter (L - d) relationships are thought to influence species competitiveness by affecting light capture. Unfortunately, little is known about how the H vs. D and L vs. d scaling exponents are related to tree performance (defined in the context of growth vigor) in competition.

Methods: Using data from field surveys of 1547 individuals and destructive sampling of 51 trees with 1086 first-order branches from a high-density *Pinus massoniana* forest, we explored whether the H vs. D and the L vs. d scaling exponents respectively differed numerically across tree performance and branch vertical position in crowns.

Results: The results indicated that (1) the H vs. D scaling exponent decreased as tree performance declined; (2) the L vs. d scaling exponent differed across tree performance classes (i.e., the scaling exponent of “inferior” trees was significantly larger than that of “moderate” and “superior” trees); (3) the L vs. d scaling exponent decreased as branch position approached ground level; and (4) overall, the branch scaling exponent decreased as tree performance improved in each crown layer, but decreased significantly in the intermediate layer.

Conclusions: 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 new insights into potential mechanisms of tree growth variation (and even further mortality) under competition in subtropical forests.

KEYWORDS

allometry, branch length-diameter, competition, height-diameter, intraspecific variation, Masson pine, Pinaceae, scaling, tree growth vigor

Competition is a fundamental process affecting the structure and development of plant communities (e.g., Tilman, 1982; Niklas and Hammond, 2013; Iida et al., 2016; Rozendaal et al., 2020). In addition to natural disasters, individuals are eliminated via inter- and intraspecific interactions, among which conspecific interactions induce intense competitive pressure, especially in the early stages of succession (Olivier et al., 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. Because both tree height and branching patterns are related to light interception (Kohyama and Takada, 2012), crown form is an important factor related to tree competition and mortality (Arellano et al., 2019). Hence, a potentially deeper understanding tree competition

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strategies and mechanisms of tree growth variation (and even further mortality) requires an exploration of whether differences in tree performance are correlated with morphometric differences in crown architecture.

Multiple traits and metrics have been used to dissect and quantify ecological processes (Paal et al., 2020). Scaling relationships provide one method to explore the link between tree performance and plant architecture using integrated paired architecture characteristics, e.g., the height-to-diameter (H vs. D) scaling relationship (e.g., McMahon, 1973; Niklas, 1995). From a mechanistic perspective, 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, MTE 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 vs. D) scaling relationship has been applied to describe the strategies both theoretically and empirically (Zhang et al., 2020a). For example, the elastic stability model assumes tree height should scale as $2/3$ of the trunk diameter (i.e., the H vs. D scaling exponent is 0.666) due to mechanical constraints (McMahon, 1973). The MTE supports the $2/3$ exponent for trees, but not for seedlings (Enquist et al., 2007). The growth-hydraulic model shows that the numerical value of the H vs. D scaling exponent differs across species and tree size (Niklas and Spatz, 2004). Numerous empirical research showed that the H vs. D scaling exponent changes among and within species (Feldpausch et al., 2011; Loubota Panzou et al., 2018; Mensah et al., 2018; Zhang et al., 2019a). Previous studies indicated that trees can alter their architecture and thus their strategy to compete with rivals (Lintunen and Kaitaniemi, 2010; Zhang et al., 2020). For example, it was widely accepted that competition can alter the numerical values of scaling exponents. Lines et al. (2012) reported that plants invest more in height growth when under intenser competition. Qiu et al. (2021) demonstrated that the H vs. D scaling exponent of Ponderosa pine increases as a function of competition. Variations in the H vs. D relationship in turn influence the competitiveness of trees (Poorter et al., 2003; del Río et al., 2019) because differences in trunk height and crown shape affect the occupation of space and light interception (Osunkoya et al., 2007). However, how tree performance (defined in the context of growth vigor) is linked to the H vs. D scaling 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 issue is whether the H vs. D scaling relationship differs as a function of tree performance.

To answer this question, we determined the numerical value of the intraspecific H vs. D scaling exponent across different classes of tree performance. Light is often the primary limiting factor in forest, and trees featured with faster height growth have competitive advantages (Ford, 2014). Hence, we hypothesized that the H vs. D

scaling exponent would decrease as tree performance declines.

In addition, the first-order branches are also important determinants of tree architecture and light capture (Loehle, 2016; Kunz et al., 2019). Therefore, tree performance in the context of the interactions among first-order branches was also examined. We focused on branch traits such as the growth in length with respect to the growth in diameter, which changes with respect to the relative position of a branch in the depth of the crown (Umeki and Seino, 2003; Lemay et al., 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 et al., 2016; Kaitaniemi et al., 2020). Additionally, branch traits also respond to competition and thus alter the tree competition strategy (Lintunen and Kaitaniemi, 2010; Wang et al., 2018). However, to the best of our knowledge, no report has linked branch length with respect to branch diameter (the L vs. d scaling relationship) to tree performance.

Therefore, an important second question is whether the branch L vs. d scaling exponent differs across tree performance and branch position. Noting that architectures that invest more in extending crown width facilitate the interception of horizontal light and crown width linearly increases with tree height (Xu et al., 2019), we hypothesized that the L vs. d scaling exponent of superior trees would be numerically greater than that of inferior trees and that the branch L vs. d scaling exponent would decrease as the position of branches within a crown approaches ground level.

To specifically address the two aforementioned hypotheses, we determined the H vs. D and the L vs. d scaling relationships of conspecific trees across different performance classes (for criteria, see Materials and Methods), and the branch scaling relationships in different crown layers (upper, intermediate, and lower) in a high-density aerial seeded Masson pine (*Pinus massoniana*, Pinaceae) forest. This uniform and almost even-age high-density forest provided an ideal living laboratory for investigating the linkage between tree performance and the two architecture traits (H vs. D and L vs. d) because of the near homogeneity of abiotic environmental factors.

MATERIALS AND METHODS

Study area description

This study site in Luoxi Town, Taihe County, Jiangxi Province, China (114°47'37"E, 26°50'59.14"N) has a subtropical monsoon humid climate with a mean annual precipitation of 1438 mm, a mean annual temperature of 18.9°C, and a mean annual relative humid of 79% (<http://data.envbox.net/>). The soil is a red soil developed from a quaternary red clay, with almost no humid layer and full of gravel on the surface due to water erosion. Masson

pine (*Pinus massoniana*, Pinaceae), an evergreen conifer, is an important species for timber production in China. Its rosin is also one of the most important raw chemical material produced in China. In addition, this species has become an excellent pioneer tree species for the afforestation of barren hills in China, due to its resistance to drought and barrenness and strong adaptability. Consequently, aerial seeding of Masson pine is a widely established practice in southern China to limit intensive soil erosion and accelerate the restoration of forest vegetation (Xiao et al., 2015).

Sampling measurement protocols

Two plots (20 × 60 m and 20 × 50 m) were established in a forest with a uniform slope (14°) and aspect (336° [i.e., 0 to 360° 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 using a measuring tape) and tree height (H) (using a telescopic measuring pole). In addition, recently dead trees were similarly measured. The performance of trees (i.e., growth vigor) was sorted into different categories using the criteria of Simard (1993): (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) superior, vigorous shoot growth, high leaf area, long needles, deep green color. We merged the moribund and poor classes into one inferior class because these trees have little or no chance for survival. The result was three growth vigor classes (inferior, moderate, and superior) for living trees. Subsequent measurements of aboveground biomass and growth rates were consistent with the visual identifications of growth vigor (Table 1). Biomass and growth rates 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 rates as tree performance declines reinforced the premises of our research ($P < 0.01$; Table 1). Before using the criteria of Simard to assess tree performance in plots, we sampled 15 trees (5 replicates × 3 classes) next to the sample plot for a preliminary test and found that biomass and growth rate differed significantly among the three performance classes.

TABLE 1 Aboveground biomass and mean growth rate (mean ± SE, $n = 17$) of trees of different performance (growth vigor) classes. Different lowercases denote significant differences among classes at the 0.05 level (one-way ANOVA).

Growth vigor	Aboveground biomass (g)	Growth rate (mm yr ⁻¹)
Inferior	2482.51 ± 158.43 c	4.51 ± 0.36 c
Moderate	4466.34 ± 242.91 b	6.35 ± 0.30 b
Superior	6727.18 ± 284.23 a	8.03 ± 0.38 a

The tree density in our study plot was 8264 individuals per hectare when surveyed in August 2018. Though we acknowledge there were a few indigenous *P. massoniana* before seeding and a few recruitments after sowing, most trees were of the same age (12 years old as determined by the rings from our destructively sampled trees). Although a few specimens of *Toxicodendron succedaneum* and *Rhus chinensis* were scattered in the forest and were measured, only *P. massoniana* was analyzed due to the negligible number of other species.

Statistical analyses only included data for trees equal to or taller than 3 m ($H \geq 3$ m) because (1) trees shorter than 3 m were recruitments and evidently younger than other trees and (2) trees shorter than 3 m were completely suppressed and had very little influence on taller trees. Using the aforementioned protocols, we used 1547 Masson pine (1458 living and 89 dead) to ascertain how the H vs. D scaling relationship was related to tree performance.

To evaluate biomass and the L vs. d scaling relationship, we destructively sampled 17 representative trees from each of the three tree performance classes ($N = 17$ trees × 3 classes = 51 trees, except for dead trees). For each tree, healthy and mature needles were collected in the four cardinal directions at one, two, and three quarters of the crown spread (Figure 1A). Branch segments (~10 cm) were collected from representative intact branches in the four cardinal directions acropetally outward from the base to the tip. Three segments were cut from sites at one, two, and three quarters of the total branch length (Figure 1B). A 5-cm-thick transverse section was cut at each meter along the length (height) and at breast height (1.3 m) of each trunk (Figure 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.

The diameter at 3 cm from the branch base was measured as branch diameter (d) for each branch; the distance from branch base to the apex was measured as length (L). The distance from the base of each branch to the tree apex was also measured for each destructively sampled tree. The total fresh mass of the trunk, branches, and leaves of each tree was determined using a hanging scale with an accuracy of the nearest 5 g.

The fresh mass 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 mass was reached. All dried disks were polished with 120 mesh sanding paper, then scanned to generate bitmap images at a 600 dpi resolution (Epson Perfection V800 Photo scanner). The width of rings was measured with WinDENDRO (V.6.1d). The average increase in D over the last 3 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 et al., 2017).

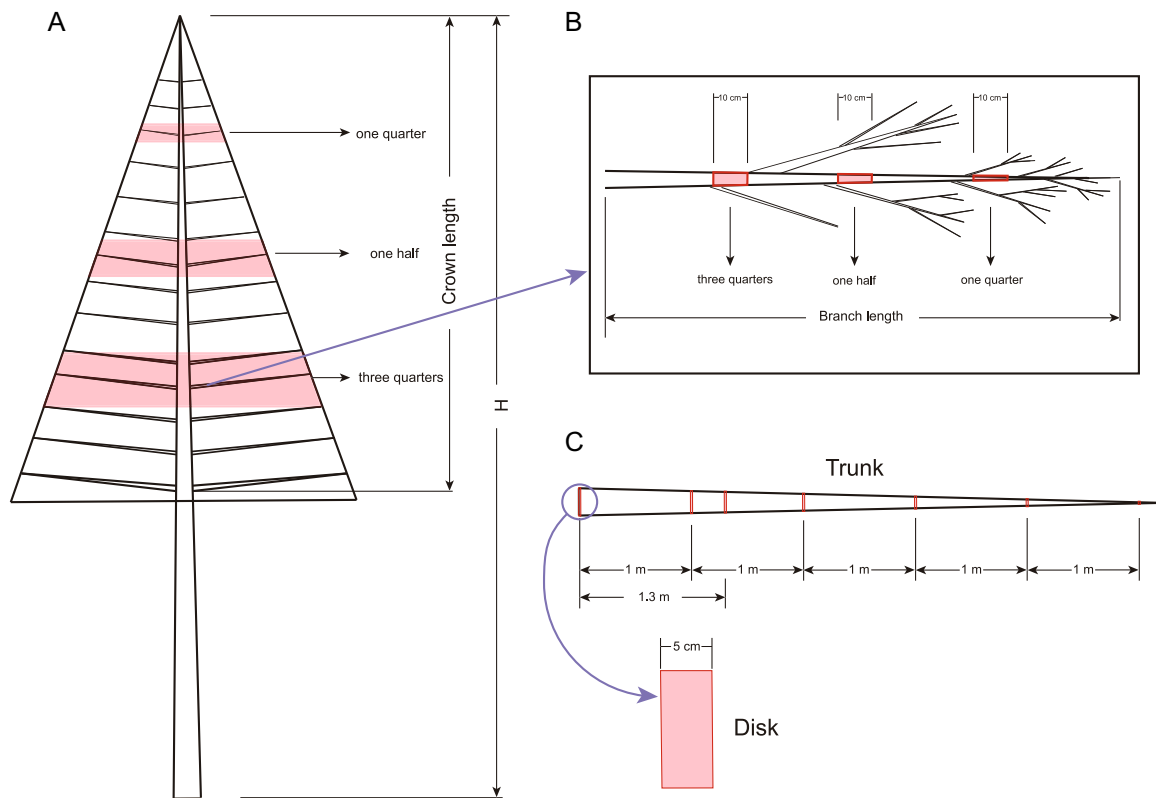


FIGURE 1 Schematic diagram of relative position of sampled (A) leaves and branches in crown, (B) branch segments on branch, and (C) disks on trunk.

Statistical analyses

The dry mass content (DMC) of each sample was calculated as $DMC = (M_{FS} - M_{DS}) / M_{FS}$, where M_{FS} and M_{DS} are the fresh mass and dry mass of the corresponding samples, respectively. We multiplied the total fresh mass 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 H and D and between branch length (L) and diameter (d) as $y = \beta x^\alpha$, where y represents H or L , x represents D or d , β is the normalization constant, and α is the scaling exponent (Niklas, 1994). To stabilize the variance, we log-transformed the data as $\log y = \log \beta + a \log x$ (Niklas, 1994). Standardized major axis (SMA) regression protocols were used for the log-transformed data to determine the numerical value of scaling exponents (a) and normalization constants ($\log \beta$) because x and y are biologically interdependent variables (Niklas, 1994; Smith, 2009). The heterogeneity of the numerical values of any two scaling exponents was deemed significant when the 95% confidence intervals did not overlap. One-way analyses of variance (ANOVA) with Fisher's least significant difference (LSD) method 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 environment R version 3.6.0 (R Core Team, 2019); SMA regression and multiple comparison for the heterogeneity of parameters was performed using the package smatr version 3.4-8 (Warton et al., 2012). All tests for heterogeneity were based on $P < 0.05$.

RESULTS

Trunk H vs. D scaling exponents among tree performance classes

The H vs. D scaling exponents numerically differed as a function of tree performance. Specifically, a decreased as tree performance declined ($P < 0.001$; Table 2, Figure 2B). The scaling exponent of superior trees was significantly larger than that of moderate trees ($a = 0.58$, 95% CI = 0.54–0.62, $P < 0.001$ and $a = 0.51$, 95% CI = 0.49–0.53, $P < 0.001$, respectively), inferior trees ($a = 0.49$, 95% CI = 0.46–0.52, $P < 0.001$), and dead trees ($a = 0.43$, 95% CI = 0.36–0.50, $P < 0.001$). No significant differences in the H vs. D scaling exponent were found among moderate, inferior, and dead trees ($P > 0.05$). Regression of all the data for living trees yielded H vs. D scaling exponent of 0.47 (95% CI = 0.46–0.48, $P < 0.001$), which was similar to that of the dead and inferior trees, but significantly different from that of moderate and superior trees (Table 2, Figure 2A).

TABLE 2 Summary of standardized major axis regression results for tree height (H) versus diameter at breast height (D) among tree performance (growth vigor) classes. The “Living” group is pooled data for the inferior, moderate and superior trees. Different lowercase denotes significant differences among groups at the 0.05 level.

Group	n	α (95% CI)	Log β (95% CI)	R^2	P
Dead	89	0.425 (0.360, 0.502) bc	0.419 (0.393, 0.445)	0.382	<0.001
Inferior	462	0.491 (0.463, 0.520) bc	0.419 (0.405, 0.432)	0.600	<0.001
Moderate	704	0.507 (0.485, 0.529) b	0.389 (0.374, 0.404)	0.658	<0.001
Superior	292	0.579 (0.543, 0.618) a	0.290 (0.258, 0.322)	0.687	<0.001
Living	1458	0.469 (0.456, 0.482) c	0.412 (0.403, 0.420)	0.714	<0.001

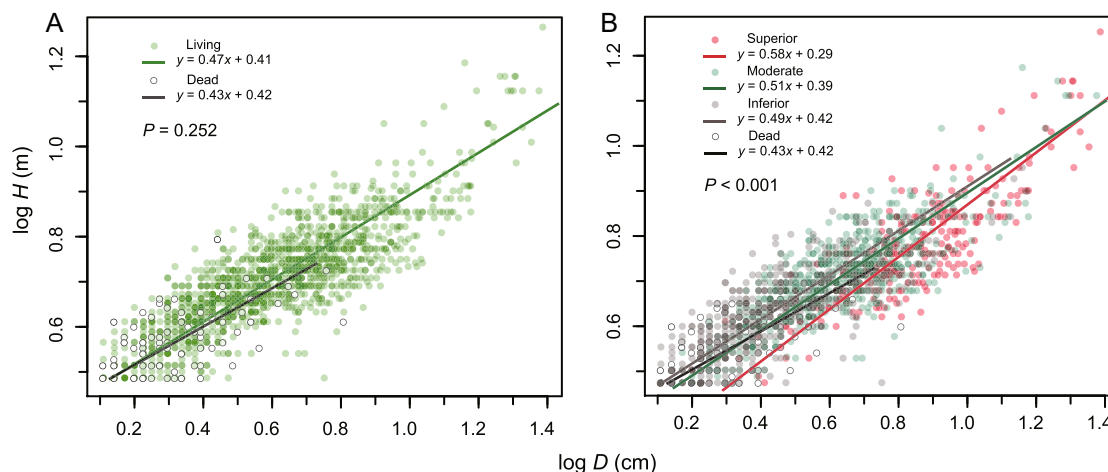


FIGURE 2 Relationships of tree height (H) and diameter at breast height (D) for (A) pooled data (living and dead) and (B) tree grouped by performance (growth vigor) classes. Statistical parameters for standardized major axis regressions are provided in Table 2. P -values indicate the heterogeneity of the scaling exponent among groups (H_0 : scaling exponents are equal).

The branch L vs. d scaling exponent among tree performance classes and branch position

The numerical value of the branch L vs. d scaling exponent for the pooled data was 1.31 (95% CI = 1.27–1.35, $P < 0.001$; Table 3, Figure 3A). The scaling exponent, however, differed significantly across the three performance classes ($P = 0.004$; Figure 3B). The L vs. d scaling exponent significantly decreased from 1.50 (95% CI = 1.42–1.59, $P < 0.001$) for inferior trees to 1.33 (95% CI = 1.25–1.41, $P < 0.001$) for moderate trees, and 1.34 (95% CI = 1.27–1.41, $P < 0.001$) for superior trees (Table 3, Figure 3B). The L vs. d scaling exponent also numerically decreased as the location of branches deepened within the crown ($P < 0.001$; Figure 4A), i.e., from 1.34 (95% CI = 1.25–1.44, $P < 0.001$) for upper branches, to 1.09 (95% CI = 1.04–1.14, $P < 0.001$) for intermediate branches, and 1.02 (95% CI = 0.97–1.08, $P < 0.001$) for lower branches (Table 3, Figure 4A).

In the intermediate and lower crown layers, the branch L vs. d scaling exponent decreased as tree performance declined (Table 3; Figure 4C, D). Furthermore, the numerical difference in the branch L vs. d exponent was significant only in the intermediate crown layer ($P < 0.001$; Figure 4B–D). Specifically, the L vs. d scaling exponent of inferior trees ($a = 1.34$, 95% CI = 1.23–1.46, $P < 0.001$) was significantly numerically larger

than that of moderate trees ($a = 1.08$, 95% CI = 0.97–1.20, $P < 0.001$) and superior trees ($a = 1.04$, 95% CI = 0.98–1.14, $P < 0.001$) (Table 3, Figure 4C).

DISCUSSION

Competition for resources among plants generates stress such that some plants cope and survive, whereas others gradually die. To understand the mechanism of plant performance under intraspecific competition, we studied two important length versus diameter scaling relationships at the individual (i.e., height versus trunk diameter, H vs. D) and branch level (i.e., length vs. diameter, L vs. d) from the perspective of crown structure. The results reported here indicate that the intraspecific scaling exponent governing the growth height with respect to the growth in trunk diameter numerically decreased ($p < 0.001$), whereas branch growth in length with respect to diameter increased ($p = 0.004$) with decreasing plant vigor (i.e., tree performance). These trends shed additional light on our understanding of the roles of crown architecture in tree competition and highlight the linkage between scaling exponents and tree growth (and even the susceptibility to mortality).

TABLE 3 Summary of standardized major axis regression results for branch length (L) versus diameter (d) across tree performance (growth vigor) classes and the vertical relative position in the crown. Different lowercase letters denote significant differences among performance classes at the 0.05 level (the range for multiple comparisons is the corresponding consecutive row with shading). Different capital letters denote significant differences among branch position groups at the 0.05 level.

Group	n	α (95% CI)	Log β (95% CI)	R^2	P
Inferior	332	1.502 (1.421, 1.589) a	0.059 (0.040, 0.078)	0.737	<0.001
Moderate	334	1.330 (1.245, 1.420) b	-0.017 (-0.030, -0.003)	0.637	<0.001
Superior	420	1.340 (1.273, 1.411) b	-0.050 (-0.062, -0.037)	0.713	<0.001
Upper	251	1.343 (1.249, 1.444) A	-0.099 (-0.119, -0.079)	0.672	<0.001
Inferior in upper	76	1.587 (1.388, 1.814) a	-0.001 (-0.063, -0.614)	0.669	<0.001
Moderate in upper	76	1.309 (1.137, 1.507) a	-0.110 (-0.136, -0.084)	0.659	<0.001
Superior in upper	99	1.355 (1.174, 1.566) a	-0.120 (-0.149, -0.091)	0.485	<0.001
Intermediate	444	1.088 (1.037, 1.141) B	-0.019 (-0.030, -0.009)	0.738	<0.001
Inferior in intermediate	143	1.341 (1.229, 1.463) a	0.046 (0.018, 0.073)	0.726	<0.001
Moderate in intermediate	132	1.076 (0.967, 1.197) b	-0.013 (-0.033, 0.006)	0.625	<0.001
Superior in intermediate	169	1.037 (0.948, 1.135) b	-0.039 (-0.056, -0.022)	0.653	<0.001
Lower	391	1.022 (0.970, 1.076) B	0.063 (0.053, 0.072)	0.725	<0.001
Inferior in lower	113	1.101 (0.982, 1.234) a	0.084 (0.064, 0.105)	0.633	<0.001
Moderate in lower	126	1.095 (0.987, 1.215) a	0.053 (0.036, 0.069)	0.658	<0.001
Superior in lower	152	0.995 (0.921, 1.074) a	0.056 (0.041, 0.071)	0.774	<0.001
All branches	1086	1.312 (1.272, 1.354)	-0.014 (-0.022, -0.006)	0.726	<0.001

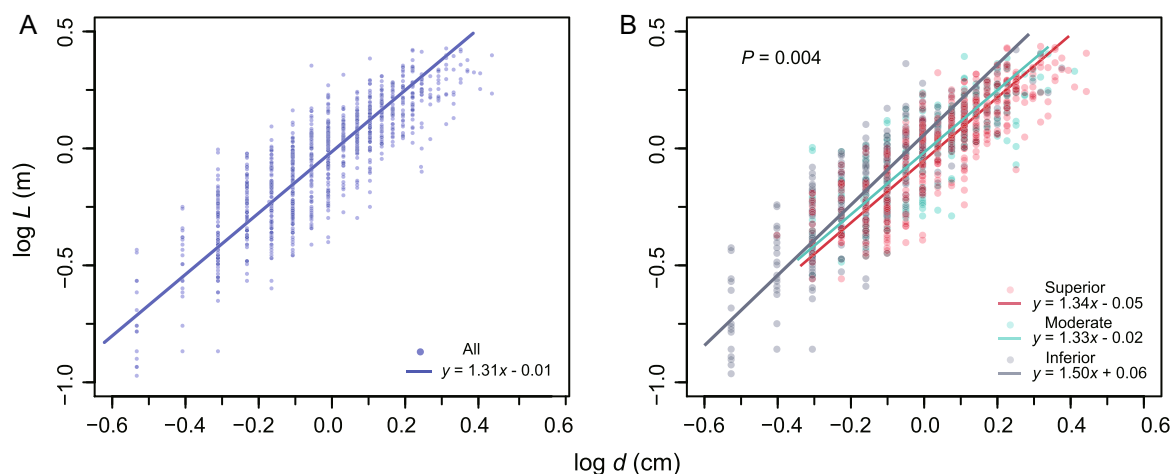


FIGURE 3 Relationships of branch length (L) and diameter (d) for (A) pooled data (living and dead) and for (B) plants grouped by performance (growth vigor) classes. Statistical parameters for standardized major axis regressions are provided in Table 3. P -values indicate the heterogeneity of scaling exponent among groups (H_0 : scaling exponents are equal).

Linkages between H vs. D scaling exponents and tree performance

Consistent with our first hypothesis, the H vs. D scaling exponent significantly differed among the different classes of tree performance (growth vigor) and numerically decreased as tree growth vigor declines (Figure 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 among living individuals (Figure 2A, Table 2). The significantly numerically higher scaling exponent of superior trees indicates that superior trees grow taller with respect to increments in trunk diameter. The lack of a significant difference in the scaling exponents of dead trees

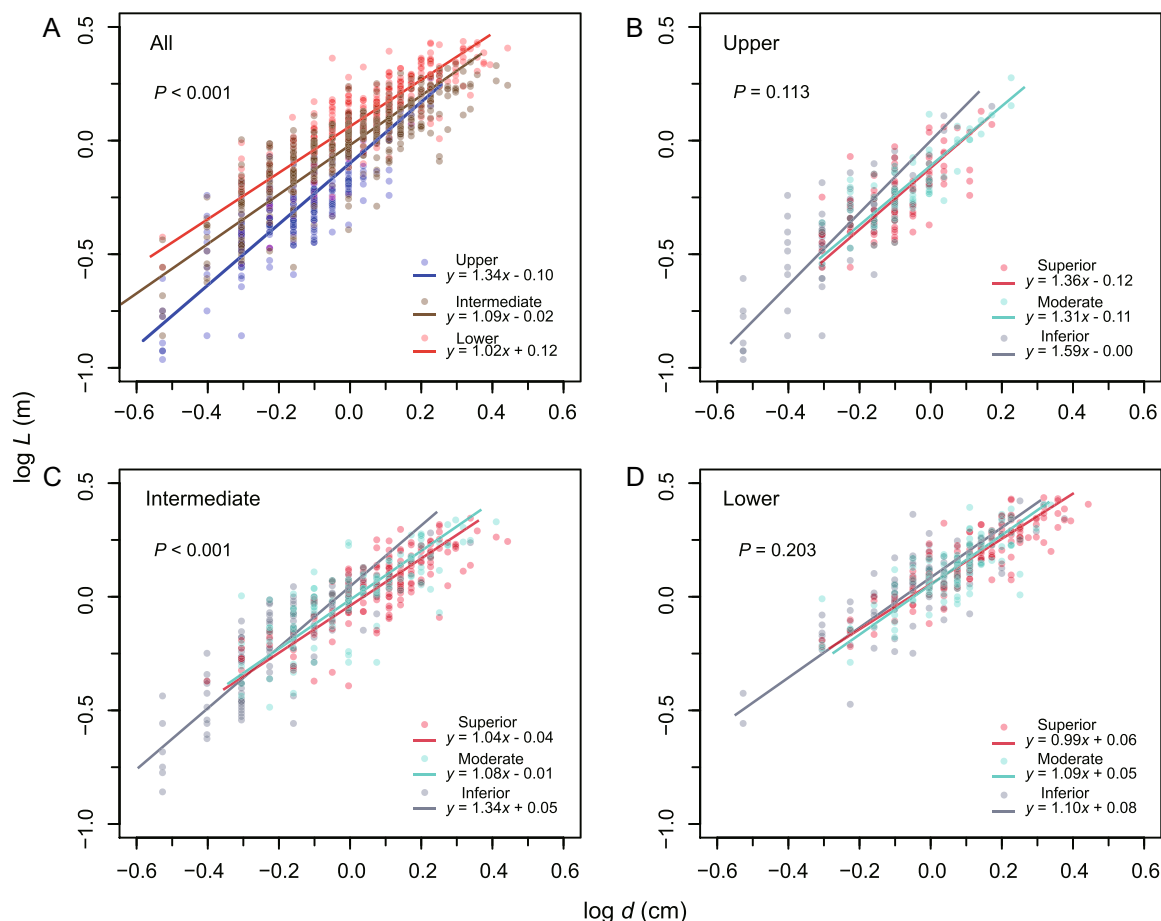


FIGURE 4 (A) Relationships of branch length (L) and diameter (d) grouped by the relative vertical position in the crown. (B–D) Relationships of L and d in the (B) upper layer branches, (C) intermediate layer, and (D) lower layer grouped by performance classes. Statistical parameters for standardized major axis regressions are provided in Table 3. P -values indicate the heterogeneity of scaling exponent among groups (H_0 : scaling exponents are equal).

and inferior trees is consistent with the observation that inferior trees are likely to ultimately die.

This study indicates that in addition to competition (Trouve et al., 2015; Qiu et al., 2021), climate (Hulshof et al., 2015; Fortin et al., 2018), forest structure (Feldpausch et al., 2011), and species composition (Mensah et al., 2018), the numerical values of the H vs. D scaling exponent differ as a function of tree performance (growth vigor) within the particular species examined in this study. In addition, the results do not support the 2/3-scaling (elastic self-similarity) law between tree height and trunk diameter at the intraspecific level, which is consistent with previous research (Russo et al., 2007; Mensah et al., 2018; Zhang et al., 2020a).

Prior research has shown that competition can stimulate vertical tree growth (Wright et al., 2004; Sun et al., 2019). Suppressed trees generally invest more in height growth relative to their radial growth compared to dominant trees in response to competition for light (Trouve et al., 2015), which results in a numerically higher H vs. D scaling exponent (Blanchard et al., 2016). This supposed generality appears to contradict the results reported here. We attribute this inconsistency to the fact that the trees in our study were

aerially sowed such that the forest examined is an almost even-aged (and species-pure) forest, indicating that the race for light began on the same starting line. Consequently, the disparities in tree height among performance classes are insufficient to have provided an obvious advantage in light capture for superior trees versus inferior trees. Conversely, in an uneven-aged forest, younger trees that establish later are completely overshadowed in the race for light by older previously established trees. Consequently, they typically grow more rapidly in height compared to their growth in girth even at the expense of reducing the ability to resist bending forces, resulting in large slenderness ratios (Niklas, 1992; 1994) and thus numerically larger H vs. D scaling exponents (Henry and Aarssen, 1999; Blanchard et al., 2016). 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 et al., 2015). The plasticity of the H vs. D scaling relationship reflects the ability of trees to self-adjust their growth responses to stressful environments (Bourque et al., 2019). In general, cadres of individual trees with numerically large H vs. D

scaling exponents manifest a competitive advantage over trees that grow more slowly in height (Ford, 2014).

Linkages between branch L vs. d scaling exponent and tree performance at different locations within the crown

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 (Figure 3B, Table 3). This phenomenology may confer an advantage with regard to crown spread and light interception (MacFarlane and Kane, 2017; Van de Peer et al., 2017; Xu et al., 2019). Longer branches (which can result in a wider crown) allow plants to capture more light (Iida et al., 2014; Loubota Panzou et al., 2018). However, in our study, the trees that tended to invest more in branch length growth over diameter growth also tended to fall into the inferior category of tree performance. One possible explanation for this trend is that the leaf biomass per branch of inferior trees is significantly smaller than that of moderate and superior trees (Figure 5). Total tree leaf area is a decisive factor in the utilization of light energy (Shi et al., 2015), and leaf area is proportional to leaf biomass. Thicker branches provide greater mechanical rigidity and thus tend to carry more leaves, which is 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 equals that of the first-order branch (Chiba, 1998), which is consistent with our results at the branch level. Another possible explanation for the variation in the scaling of branch length vs. diameter is the compensatory effect; that is, inferior trees extend their branches thereby allowing leaves to be illuminated sufficiently to compensate for their lack of leaves. Our study indicates that trees with a preferred

height growth strategy at the individual level have a competitive advantage regarding light interception. Nevertheless, at the branch level, a strategy of increasing branch diameter to sustain the mechanical loads of more photosynthetic leaves improves light acquisition. These results are in line with the trade-off between tree height gain and crown expansion (Osunkoya et al., 2007).

The data reported here are consistent with our hypothesis that the L vs. d scaling exponent numerically decreases as the location of branches deepens within the crown and differs across tree performance in the intermediate layer. The different L vs. d scaling exponents among the branches sampled from different crown layers indicates that the scaling of the L vs. d depends on location and perhaps age (because branches closer to the ground level tend to be older branches).

Previous studies indicate that branch traits such as diameter, length, and death vary as a function of the relative position of branches within a crown (Umeki and Seino, 2003; Chen and Sumida, 2017; Lemay et al., 2019). Our study highlights the co-variance of branch traits along a crown-depth gradient based on scaling relationships. The competition for light and space may be the main driver of this pattern. The space within a crown 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 (or light availability). Thus, the scaling exponent for the branches in the upper part of the crown tends to be numerically larger than that for branches lower within the crown. Interestingly, branches in the intermediate layer tend to intercept more light than those of branches above or below them because the upper branches are illuminated fully but sustain fewer leaves, whereas the lowermost branches are light-deprived because of self-shading within the crown (Osada and Takeda, 2003). Consequently, the fiercest competition for light and space within a crown might tend to be in the intermediate layer, which leads to a significant difference in the L vs. d scaling exponent in this layer among tree performance classes.

Finally, it is worth noting that the statistically significant dissimilarities in the scaling exponents among tree conspecifics assigned to different growth vigor draws attention to 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.

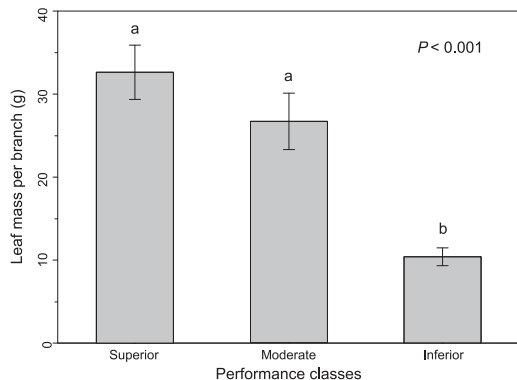


FIGURE 5 Leaf mass per branch among performance (growth vigor) classes (inferior, moderate and superior). Error bars indicate standard errors. Different lowercase letters denote significant differences among groups at the 0.05 level (one-way ANOVA).

CONCLUSIONS

Overall, the data show that tree performance correlates with tree architectural traits as defined by the scaling exponent at both the individual tree and branch levels; that is, trees with

a numerically larger H vs. D and a numerically smaller L vs. d scaling exponent grow more vigorously and thus perform better in competition. In addition to the numerical decrease in the L vs. d scaling exponent as the position of branches deepens within the crown, the data show that the strongest linkage between the L vs. d scaling exponent and tree performance is determined by branches that are located intermediately within the crown. These findings improve our understanding of tree competitive strategies and potential mechanisms of tree growth variation and highlight the importance of intraspecific variation in scaling exponent. Nevertheless, other species need to be analyzed similarly to determine whether the trends reported here can be extended to other species.

AUTHOR CONTRIBUTIONS

G.Z., Q.Y., and G.W. conceived and designed the experiments. G.Z. and Q.Y. performed the experiments. G.Z. and K.J.N. analyzed the data. G.Z., K.J.N., K.X., and Q.Y. wrote the paper.

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DATA AVAILABILITY STATEMENT

See Appendix S1 for raw data of tree height (H) and diameter at breast height (D), branch length (L), and branch diameter (d).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Raw data for tree height (H) and diameter at breast height (D), branch length (L), and branch diameter (d).

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