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Impact of canopy vertical height on leaf functional traits in a *Cunninghamia lanceolata* common garden experiment in Dagangshan

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Abstract

Background: Plant functional traits represent resource acquisition strategies, and, consequently, reflect ecosystem function. As a critical focus on functional trait research, the study of intraspecific variation and vertical gradients in canopies can better reveal plant adaptation mechanisms to environmental conditions. In this study, we examined five provenances of *Cunninghamia lanceolata* in the common garden of Dagangshan, Jiangxi, measured and analyzed nine functional trait indicators: the leaf dry matter content, relative chlorophyll content, specific leaf area, leaf tissue density, water use efficiency, leaf carbon content, leaf nitrogen content, carbon-to-nitrogen ratio, and equivalent water thickness.

Results: The results revealed that canopy height has a minor effect on the variation in leaf functional traits, with most of the variation attributed to geographic provenances. Notably, 50% of the leaf functional traits presented significant correlations, which were associated mainly with photosynthetic capacity-related traits. The correlations of leaf functional traits between the average canopy values and the middle part of the canopy are similar.

Conclusion: The influence of canopy height on leaf functional traits in subtropical *Cunninghamia lanceolata* artificial forests is limited, but the provenances effect had a certain impact on the leaf functional traits. The consistency of trait relationships between middle part and the entire canopy making it feasible to analyze forest ecosystem functions by collecting leaf samples from the middle canopy. This study provides scientific evidence for research on the functional dynamics of *Cunninghamia lanceolata* artificial forest ecosystems and the selection of superior provenances.

Keywords: geographical provenances ; carbon-to-nitrogen ratio; specific leaf area; equivalent water thickness; water use efficiency

1. Introduction

Plant functional traits elucidate the mechanisms of species coexistence and community dynamics within forests [1]. Leaves, which are sensitive to environmental changes [2], exhibit functional traits that are relatively straightforward to measure, making them crucial for research on plant functional traits [3]. Since Wright et al. (2004) combined a series of related leaf functional traits to represent plant resource balancing strategies and proposed the Leaf Economic Spectrum (LES) [4], this theory has been extended to include traits of wood and other plant organs [5-7]. The Plant Economic Spectrum (PES) can predict the dynamics of community composition and ecosystem functions [8]. Reich (2014) found a broad trade-off between slow growth (conservative strategy) and rapid growth (acquisition strategy) in species by integrating the characteristics of roots, stems, and leaves, including traits related to water, carbon, and nutrient resources [9]. The theory of plant economic spectrum provides a basic theoretical framework for understanding plant adaptation strategies by integrating the trade-off between plant functional traits in resource acquisition and

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resource conservation [10-11]. Leaves have received the most widespread attention due to their ease of sampling and measurement [12]. Leaf traits not only reflect resource acquisition capabilities but also characterize plant survival strategies [13,14]. The primary categories of research on plant leaf traits include those on morphological, physiological, biochemical, and stoichiometric traits [15]. The individual or combined effects of these different traits can reveal adaptation strategies to environmental conditions [16,17].

Research has focused on the impact of environmental factors on leaf functional traits [18,19], as well as differences in species traits [20] and adaptation strategies at a regional scale [21]. However, investigations into trait variation and adaptation characteristics within small habitats at the individual scale are relatively limited. Light is a key factor influencing plant growth and development, and is closely linked to photosynthesis [22]. Previous studies have indicated that light intensity affects plant functional traits [23]. Notably, the nitrogen and phosphorus contents per unit leaf area of canopy plants are 60% and 90% higher than the average contents in understory plants, respectively [24]. As the plant part that is most directly connected to the external environment, the canopy itself has altered light intensity because of its shape and structure [25]. Consequently, variations in light, temperature, moisture, and other conditions may occur at different heights within the canopy [26]. Leaf functional traits may change in response to these habitat variations [27]. Some studies have shown that leaves situated in the upper part of the canopy tend to have smaller leaf areas, greater leaf thickness, and higher specific leaf weight, whereas leaves in the lower canopy exhibit higher specific leaf area and nitrogen content to increase resource utilization efficiency [28,29]. Nonetheless, few studies have examined the differences among multiple traits and the relationships among functional traits along the vertical gradient of the canopy.

Most studies have focused on the variation in plant functional traits at the community level along environmental gradients [30,31], often neglecting the variation in individual functional traits within species. The adaptability of individuals to the micro-environment leads to variations in plant functional traits [32,33], whereas genetic differences, phenotypic plasticity, and other factors result in intraspecific variation [34,35]. Many studies have demonstrated that nearly one-third of trait variation within a community stems from intraspecific trait variation [36,37], which is especially pronounced when the number of species in the community is low or when environmental stress is minimal [38]. In the process of adapting to diverse environments, plants develop geographical provenances [39]. By transplanting these provenances from different regions into common gardens, researchers can observe variations in growth [40], enabling them to elucidate the adaptation strategies of these provenances to identical environmental conditions, which is a crucial consideration for selecting superior provenances in the context of climate change [41,42]. *Cunninghamia lanceolata* (commonly known as Chinese fir), serves as an important timber resource, is used for artificial afforestation in southern China, which is widely distributed in 19 provinces [43]. Chinese fir is the main dominant tree species in the national plantation forests of China [44]. China has conducted extensive long-term research on the provenances of Chinese fir, with studies examining the variation in growth, resistance, and functional traits [45]. In particular, investigating leaf functional traits at different canopy heights from various provenances provides valuable insights into the developmental characteristics and growth strategies of tree canopies across these provenances.

Leaves from middle part of the canopy which exposed to sunlight are often collected to represent the functional traits of individual plants or entire communities [46, 47]; however, the variation in functional traits along the vertical gradient of the canopy and among different individuals is often overlooked. This study focused on five provenances in the Chinese fir common garden of Dagangshan, Jiangxi. By measuring and analyzing the functional traits of leaves at various canopy heights of these provenances, we aim to achieve the following objectives: (1) to assess the differences in leaf functional traits among Chinese fir provenances; (2) to examine the variation in leaf functional traits with vertical height within the canopy and determine whether differences exist among provenances; and (3) to explore the relationships among leaf functional traits.

2. Materials and methods

2.1. Study site

This study was conducted in Dagangshan National Key Field Observation and Research Station for Forest Ecosystem, JiangXi Province, China (114° 31' 23" E ~114° 44' 31" E, 27° 32' 2" N ~27° 49' 31" N). The mean annual air temperature and precipitation are 15.8 °C and 1600 mm, respectively. Most precipitation occurs from April to June, accounting for 45% of the annual precipitation. In 1981, the Chinese Academy of Forestry conducted a geographical provenance experiment of Chinese fir at here [45], which established a common garden containing 183 Chinese fir provenances. In this study, we selected 5 provenances growing in the common garden for 41 years under the same climatic and soil conditions (Table 1). The height (H) and diameter at breast height (DBH) of each selected individual were measured before sampling.

Table 1. Origin of provenances, tree height (m; mean $\pm$ standard deviation) and diameter at breast height (cm; mean $\pm$ standard deviation) of sample trees. Where H indicates the height of sample trees, DBH indicates the diameter at breast height of sample trees. Different letters indicate significant differences among provenances ($P < 0.05$), same letters indicate non-significant differences among provenances ($P > 0.05$).

Provenances	H(m)	DBH(cm)
ZJYH(Zhejiang Yunhe)	16.17 $\pm$ 1.84a	21.54 $\pm$ 3.52a
JXAF(Jiangxi Anfu)	18.33 $\pm$ 1.65a	28.09 $\pm$ 3.27a
JXLA(Jiangxi Lean)	18.10 $\pm$ 1.37a	23.76 $\pm$ 1.88a
HBWF(Hubei Wufeng)	17.67 $\pm$ 2.36a	25.83 $\pm$ 6.38a
GXYF(Guangxi Yongfu)	17.50 $\pm$ 1.08a	22.27 $\pm$ 2.54a

2.2. Samples collection

In this study, considering the actual conditions and heights of the selected provenances, the canopy was categorized vertically into three layers: the lower layer (less than 6 meters above ground), the middle layer (between 6 and 11 meters above ground), and the upper layer (greater than 11 meters above ground). In September 2023, three individuals from each provenance were selected as replicates (total 15 Chinese fir individuals), the growing condition of these trees are basically the same, and the trees selected from each provenance have good growth conditions and are basically consistent. Leaves were collected from the upper, middle, and lower layers of the canopy for each individual, by pruning and climbing techniques. During the sampling process, healthy branches were chosen from various layers and directions of each individual, with at least 50 mature, healthy, and intact leaves at each layer were collected from this year's growth segments, which were immediately placed in envelopes. Bring back to the laboratory for measuring functional traits within two hours.

2.3. Measurement of functional traits

Nine functional traits of leaves were chosen for measurement in this study: leaf dry matter content (LDMC, g/kg), relative chlorophyll content (SPAD), specific leaf area (SLA, cm²/g), leaf tissue density (LTD, g/cm³), water use efficiency (WUE, μ molCO₂/molH₂O), leaf carbon content (LCC, g/kg), leaf nitrogen content (LNC, g/kg), carbon-to-nitrogen ratio (C:N), and equivalent water thickness (EWT, mm). The

methods for obtaining basic data on leaf functional traits followed the guidelines of Cornelissen [46] and Perez-Harguindeguy [47]. After the petiole removed, the fresh weight of the leaves (LFW) was measured via an electronic balance (the accuracy was 0.001g). The chlorophyll content was assessed at three different positions (upper, middle, and lower) on the leaf using a SPAD-502, with the average value taken as the chlorophyll content. Leaf images were obtained using a CanoScan scanner (the image resolution is 300DPI), and the area of the leaves (LA) was calculated using the image processing software ImageJ. The thickness of each leaf was measured with a caliper at three random positions, with the average value taken as the leaf thickness (LT).

The processed leaves were first subjected to removing green at 105 °C and then dried to a constant weight at 65 °C. Afterward, the leaves were weighed using an electronic balance to obtain the dry weight (LDW). A grinder was used to pulverize the samples, which were then sieved through a 100-mesh screen. The leaf carbon content was determined using the dichromate heating method, whereas the leaf nitrogen content was evaluated using a Kjeldahl nitrogen analyzer. The stable carbon isotope values of the leaves were measured using a stable isotope ratio mass spectrometer.

The calculation formulas for functional traits are as follows. LDMC was calculated by LDW and LFW, referring to equation 1, SLA was calculated by LA and LDW, referring to equation 2, LTD was calculated by LDW, LT, and LA, referring to equation 3, EWT was calculated by LFW, LDW, and LA, referring to equation 4.:

$$\begin{aligned} \text{LDMC} &= \text{LDW} / \text{LFW}_{(1)}, \\ \text{SLA} &= \text{LA} / \text{LDW}_{(2)}, \\ \text{LTD} &= \text{LDW} / (\text{LT} * \text{LA})_{(3)}, \\ \text{EWT} &= (\text{LFW} - \text{LDW}) / \text{LA}_{(4)}, \end{aligned}$$

The WUE was calculated by the relative abundance of $^{13}\text{C}/^{12}\text{C}$ in the sample, referring to equation 5, 6, and 7, The calculation formula for functional traits are as follows [48]:

$$\delta^{13}\text{C}_p = \left(\frac{R_{sam}}{R_{std}} - 1 \right) \times 1000\text{‰} \quad (5)$$

where R_{sam} is the relative abundance of $^{13}\text{C}/^{12}\text{C}$ in the sample; and R_{std} is the relative abundance of $^{13}\text{C}/^{12}\text{C}$ in the internationally recognized standard substance VPDB (Vienna Pee Dee Belemnite)

$$\text{WUE} = \frac{C_a (b - \Delta^{13}\text{C})}{1.6(b - a)} \quad (6)$$

$$\Delta^{13}\text{C} = \frac{\delta^{13}\text{C}_a - \delta^{13}\text{C}_p}{1 + \delta^{13}\text{C}_p / 1000} \quad (7)$$

where C_a is the atmospheric CO_2 concentration; a is the fractionation coefficient during the diffusion process of CO_2 ; b is the fractionation coefficient during the carboxylation reaction; 1.6 is the conductivity

ratio of stomata to water vapor and CO_2 ; $\Delta^{13}\text{C}$ is the discrimination ratio of plant carbon isotopes; $\delta^{13}\text{C}_p$ is the carbon isotope ratio of plant leaves; and $\delta^{13}\text{C}_a$ is the carbon isotope ratio of CO_2 in the atmosphere.

2.4. Data analysis

All data were expressed as the mean $\pm$ standard error (SE). After a normality test was conducting on the data, One-Way analysis of variance (ANOVA) was conducted to examine the significant differences of various traits among different vertical heights or provenances. The Pearson correlation coefficient was used to assess the correlations among functional traits. The significance level for the tests was set at $P=0.05$. We also examined the differences between functional traits at different levels and average canopy traits. All the statistical analyses were conducted using SPSS software (version 22.0, IBM SPSS, Chicago, Illinois), figures are made on <https://cnsknowall.com>.

3. Results

3.1. Vertical variation patterns of leaf functional traits

Our analysis revealed no significant differences ($P>0.05$) in the nine selected leaf functional traits among the different canopy heights (Figure 1). Overall, LDMC, LTD, WUE, LCC, LNC, C:N, and EWT in the upper canopy were slightly higher than those in the lower and middle canopies. Conversely, SLA was lower in the upper canopy than in the other heights, whereas SPAD values were slightly lower in the lower canopy than in the upper canopy but higher than in the middle canopy. Leaves situated in the middle of the canopy presented the lowest values for LDMC, SPAD, LCC, LNC, C:N, and EWT among the three heights..

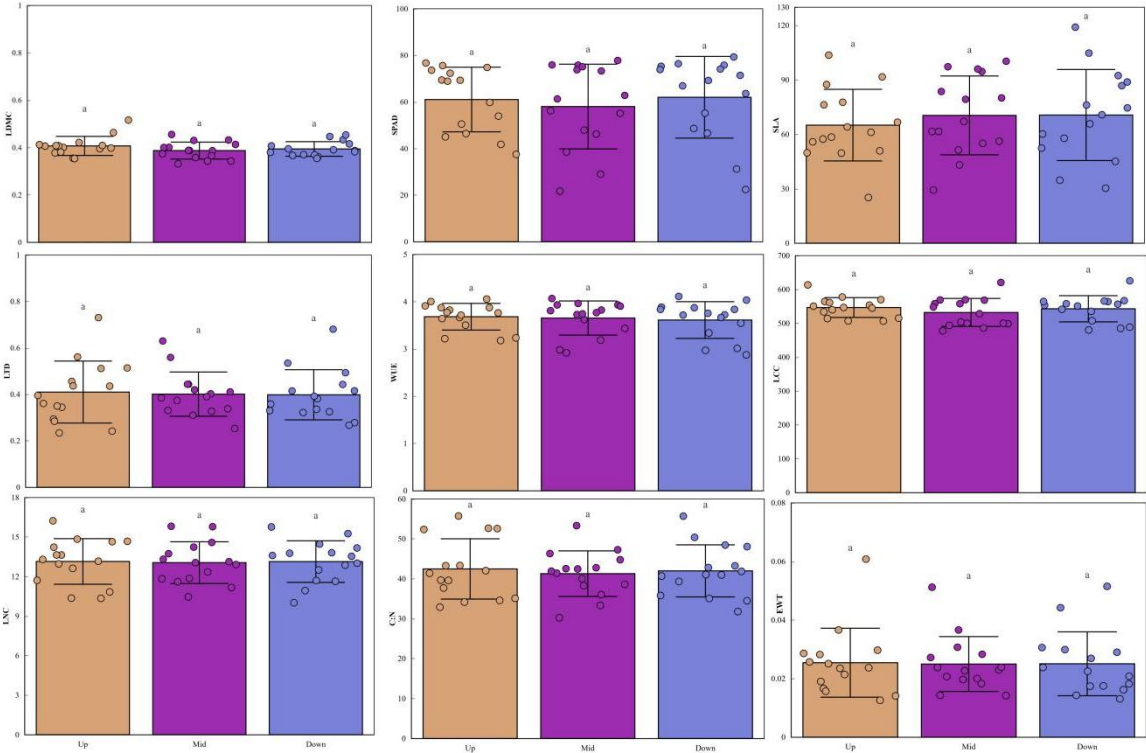


Fig. 1. Leaf functional traits at different canopy heights. Where LDMC, SPAD, SLA, LTD, WUE, LCC, LNC, C:N, and EWT represent leaf dry matter content, relative chlorophyll content, specific leaf area, leaf tissue density, water use efficiency, leaf carbon content, leaf nitrogen content, carbon-to-nitrogen ratio, and equivalent water thickness, respective. Data represent the mean $\pm$ S.E., and different lowercase letters above error bars indicate significant different among canopy heights by One-way ANOVA test at the P = 0.05 level

3.2. Differences in leaf functional traits among provenances

We calculated the average leaf functional traits from the upper, middle, and lower canopy layers of the same provenance to represent the leaf functional traits of that provenance, investigating the differences in functional traits among various provenances (Figure 2). There were no significant differences in LDMC among the five provenances ($P>0.05$). The SPAD value of GXYF was significantly lower than those of the other provenances ($P<0.05$). The SLA of HBWF and GXYF were higher than other provenances ($P<0.01$). JXAF, JXLA, and GXYF presented significantly greater LTD than the other two provenances ($P<0.01$). ZJYH has the highest WUE, LCC and LNC among these provenances.. With respect of the C:N ratio, significant differences were observed only between provenances JXAF and HBWF ($P<0.05$). The EWT of JXLA was the highest.

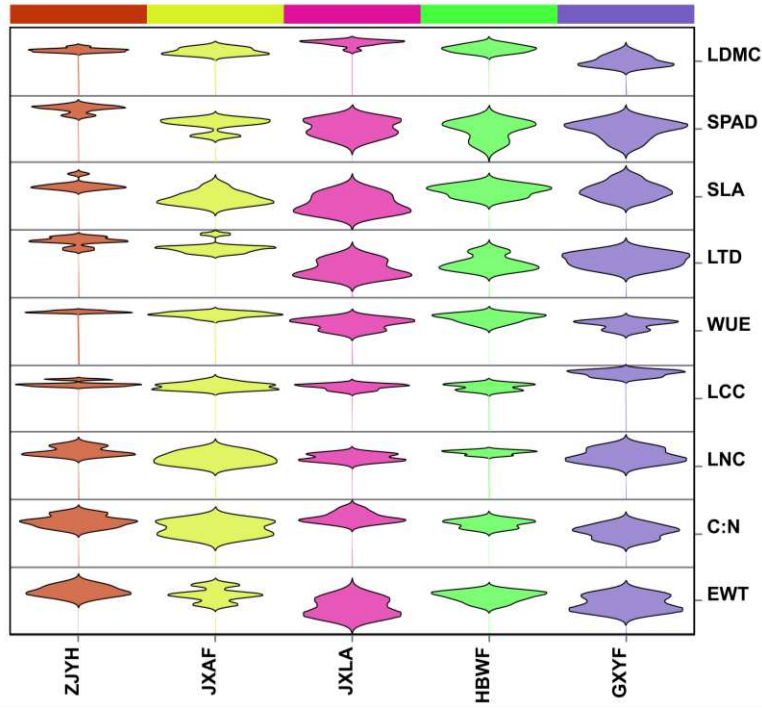


Fig. 2. Violin plots showing nine leaf functional traits of different provenances. Where ZJYH, JXAF, JXLA, HBWF, and GXYF represent the provenances from Zhejiang Yunhe, Jiangxi Anfu, Jiangxi Lean, Hubei Wufeng, and Guangxi Yongfu, respective. Refer to Figure 1 for trait abbreviations.

3.3. The combined effects of provenance and canopy height on leaf functional traits

Statistical analysis (Table 2) of the leaf functional traits across the five provenances at three different vertical positions (upper, middle, and lower) in the canopy revealed that LDMC (except for GXYF), SPAD (except for ZJYH), WUE, LCC, EWT (except for ZJYH), and C:N tended to decrease trend with increasing canopy height. In contrast, SLA, LTD, and LNC did not show pattern changes. Provenance had a significant effect on leaf functional traits (SPAD, SLA, LTD, LNC, and EWT) ($P < 0.05$), whereas the effect of canopy height on these traits was not significant.

3.4. Relationships among leaf functional traits

Overall, 50% of the leaf functional traits presented significant correlations (Figure 3A). Notably, C:N was significantly correlated with LDMC and the EWT at the $P < 0.05$ level, whereas the remaining traits were displayed highly significant correlations ($P < 0.01$). Differences in relationships exist among traits along the vertical gradient (Figure 3B~3D). Consistent relationships were found between SPAD and WUE, SPAD and EWT, as well as LNC and C:N. Although the relationships among SPAD and LCC, LTD and EWT, and WUE and LCC also remained unchanged, their significance levels varied.

In contrast to the overall results, the correlations of the leaf functional traits in the middle canopy were generally consistent with the overall findings, whereas the correlations in the lower canopy differed considerably from the overall results.

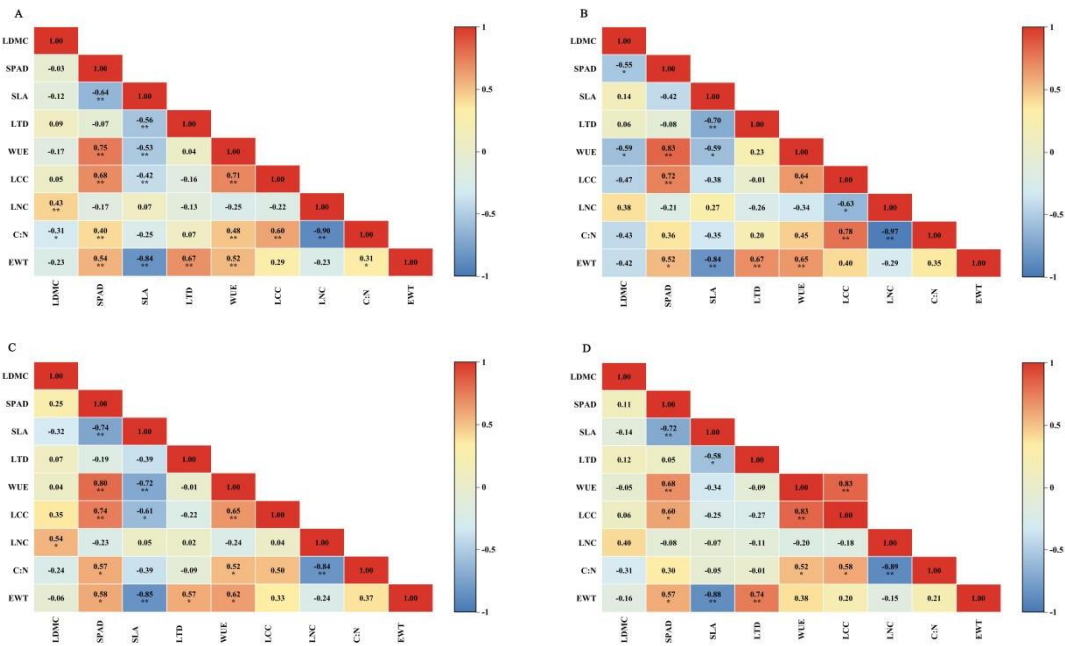


Fig. 3. Relationships among leaf functional traits at (A) overall canopy, (B) upper canopy, (C) middle canopy and (D) lower canopy. Refer to Figure 1 for trait abbreviations. * indicates a significance level of $P < 0.05$, ** indicates a significance level of $P < 0.01$.

Table 2. Leaf functional traits of different provenances at different vertical locations (Means $\pm$ SE). u, m, and d represent the locations of the upper, middle and lower of canopy heights, respectively. Refer to Figure 1 for trait abbreviations. Refer to Figure 2 for provenances abbreviations.

	LDMC(g/kg)	SPAD	SLA(cm ² /g)	LTD(g/cm ³)	WUE(μ mol/mol)	LCC(g/kg)	LNC(g/kg)	C:N	EWT(mm)
ZJYHu	408.43 $\pm$ 22.38a	71.67 $\pm$ 7.29a	62.19 $\pm$ 10.69a	0.33 $\pm$ 0.04a	3.99 $\pm$ 0.05a	598.98 $\pm$ 41.91a	13.15 $\pm$ 0.14c	45.57 $\pm$ 3.64a	0.23 $\pm$ 0.02b
ZJYHm	402.87 $\pm$ 3.64a	69.63 $\pm$ 7.37a	60.05 $\pm$ 1.54a	0.34 $\pm$ 0.01a	3.88 $\pm$ 0.05b	554.16 $\pm$ 14.45a	13.66 $\pm$ 0.07b	40.57 $\pm$ 0.92b	0.24 $\pm$ 0.01b
ZJYHd	381.44 $\pm$ 4.75a	72.2 $\pm$ 2.44a	54.94 $\pm$ 2.49a	0.32 $\pm$ 0.02a	3.84 $\pm$ 0.03b	555.69 $\pm$ 18.93a	15.93 $\pm$ 0.26a	34.90 $\pm$ 1.75c	0.29 $\pm$ 0.01a
JXAFu	411.04 $\pm$ 22.70a	77.27 $\pm$ 1.82a	45.99 $\pm$ 3.44b	0.43 $\pm$ 0.03a	3.90 $\pm$ 0.06a	558.02 $\pm$ 54.83a	12.15 $\pm$ 0.63b	46.02 $\pm$ 5.50b	0.31 $\pm$ 0.05ab
JXAFm	369.86 $\pm$ 16.70a	70.00 $\pm$ 3.50ab	52.93 $\pm$ 4.31b	0.44 $\pm$ 0.02a	3.70 $\pm$ 0.03b	564.46 $\pm$ 11.45a	10.28 $\pm$ 0.24c	54.92 $\pm$ 1.38a	0.32 $\pm$ 0.04a
JXAFd	380.05 $\pm$ 35.73a	54.50 $\pm$ 12.75b	69.71 $\pm$ 8.33a	0.45 $\pm$ 0.09a	3.49 $\pm$ 0.14c	504.88 $\pm$ 4.32a	14.12 $\pm$ 0.94a	35.84 $\pm$ 2.16c	0.24 $\pm$ 0.03b
JXLAu	396.73 $\pm$ 2.98a	75.70 $\pm$ 0.82a	29.72 $\pm$ 4.78b	0.63 $\pm$ 0.10a	4.08 $\pm$ 0.03a	551.14 $\pm$ 8.64a	13.42 $\pm$ 0.32a	41.09 $\pm$ 1.54b	0.52 $\pm$ 0.08a
JXLAm	387.46 $\pm$ 12.45a	61.97 $\pm$ 12.04ab	47.58 $\pm$ 15.89b	0.5 $\pm$ 0.16ab	3.76 $\pm$ 0.04b	560.66 $\pm$ 11.24a	11.44 $\pm$ 0.53b	49.12 $\pm$ 3.18a	0.36 $\pm$ 0.13ab
JXLAd	369.29 $\pm$ 37.89a	46.23 $\pm$ 8.42b	86.92 $\pm$ 10.57a	0.37 $\pm$ 0.02b	3.04 $\pm$ 0.16c	496.14 $\pm$ 17.07b	12.32 $\pm$ 1.15ab	40.43 $\pm$ 2.49b	0.20 $\pm$ 0.03b
HBWFu	428.26 $\pm$ 19.30a	74.93 $\pm$ 0.76a	71.39 $\pm$ 4.62a	0.31 $\pm$ 0.02a	3.68 $\pm$ 0.05a	566.73 $\pm$ 2.73a	14.09 $\pm$ 0.24a	40.22 $\pm$ 0.67a	0.19 $\pm$ 0.01a
HBWF m	403.25 $\pm$ 19.28a	67.70 $\pm$ 4.42a	96.89 $\pm$ 8.91a	0.25 $\pm$ 0.02a	3.59 $\pm$ 0.17a	542.26 $\pm$ 37.84a	13.14 $\pm$ 0.35b	41.25 $\pm$ 2.39a	0.15 $\pm$ 0.01a
HBWFd	403.75 $\pm$ 52.11a	31.07 $\pm$ 9.86b	91.68 $\pm$ 2.89b	0.35 $\pm$ 0.10a	3.08 $\pm$ 0.18b	493.91 $\pm$ 11.17b	14.47 $\pm$ 0.26a	34.14 $\pm$ 0.70b	0.16 $\pm$ 0.03a
GXYFu	373.91 $\pm$ 33.11b	54.50 $\pm$ 5.62a	86.72 $\pm$ 29.54a	0.41 $\pm$ 0.09a	3.88 $\pm$ 0.02a	532.08 $\pm$ 27.95ab	10.82 $\pm$ 0.42c	49.27 $\pm$ 4.05a	0.21 $\pm$ 0.05a
GXYF m	350.33 $\pm$ 6.43b	47.77 $\pm$ 2.38a	92.79 $\pm$ 13.81a	0.39 $\pm$ 0.05a	3.75 $\pm$ 0.03a	536.98 $\pm$ 9.34a	12.50 $\pm$ 0.14b	42.97 $\pm$ 0.31b	0.20 $\pm$ 0.03a
GXYFd	474.75 $\pm$ 35.70a	30.13 $\pm$ 7.95b	80.86 $\pm$ 13.06a	0.52 $\pm$ 0.03a	3.08 $\pm$ 0.14b	492.89 $\pm$ 19.69b	15.25 $\pm$ 0.57a	32.38 $\pm$ 2.49c	0.14 $\pm$ 0.01a

4. Discussions

4.1. Impact of canopy height on variability in leaf functional traits

In this study, we demonstrated that the impact of canopy height on leaf functional traits in Chinese fir artificial forest is limited (Figure 1). However, the result is not consistent with some researches that have revealed significant differences in leaf traits at varying heights within the canopy [49-51]. The canopy structure and leaf characteristics is seemed to be the main reason for this result.

Owing to the canopy structure is approximately conical with relatively larger inter-leaf gaps, leaves located in the middle and lower sections of the canopy also receive substantial light radiation [52,53], resulting in limited variation in traits across different canopy heights. The leaf cuticle layer of conifer species at all levels is relatively thick, which can effectively reduce water evaporation [54]. Generally, variations in light and moisture appear to be the primary factors influencing changes in leaf functional traits at different vertical heights within the canopy [55,56]. Research indicates that as canopy height increases, the specific leaf area (SLA) tends to decrease, while leaf thickness (LTD) tends to increase [57,58]; this study confirm these findings. As shown in Figure 1, leaves in the upper layer, which are exposed to a stronger light environment, typically adopt strategies such as increased thickness, increased leaf area, and stomatal closure to mitigate water loss [59], resulting in lower SLA and greater leaf water thickness (EWT). Some studies showed that shade leaves have 43.3% higher SLA than sun leaves [60], in this study, this gap had been reduced 8.57%, which mainly because of the experiment conducted within one species in a common garden. Some studies also found that LDMC did not show significant changes with the increase of canopy height [61-62], which is consistent with our results, but is inconsistent with some previous research conclusions [63-64], which may because the variation of functional traits may influenced by sampling time, sampling location, and plant selection [62]. Furthermore, the top leaves of the canopy must survive high radiation and evaporation, achieving a balance between carbon fixation and water consumption through stomatal regulation [59], leading to higher water use efficiency than that in the lower layers. The functional traits closely related to photosynthetic rates, such as leaf nitrogen content and SPAD values [59]. The content of N in leaves did not show a significant consistent change pattern with the increase of vertical height, which may be due to the comprehensive influence of factors such as light intensity, water content, wind speed, nutrient utilization mode, plant characteristics, and soil N and P element content [65]. Additionally, severe nitrogen deposition in subtropical regions of China may be an important factor affecting the results [66].

4.2. Impact of provenances on variability in leaf functional traits

In this study, we find that intraspecific differences occur in leaf functional traits among provenances, which is also demonstrated in the previous study that leaves exhibit considerable plasticity [34]. When different genetic provenances are transplanted into a homogeneous garden, the environmental heterogeneity of the provenance location results in genetic effects such as differences in functional traits [67,68].

The phenotypic plasticity of plants is closely related to the environment and is an adaptation to environmental conditions throughout evolution. Tree after long-term growth in different ecological environments undergo adaptive geographic variation to the local habitat, forming different geographic provenances [39]. In this study, LDMC, WUE, and LCC did not have significant regulatory effects on the provenances, primarily because provenances ZJYH, JXAF, JXLA, and HBWF are all located in provenance zone VII [45]. The zones are classified on the basis of the growth parameters of various provenances, and the resource utilization strategies within the same zone are relatively similar [45], leading to minimal differences. As shown in Figure 2 and Table 2, ZJYH presented relatively high LCC, LNC, WUE, and SPAD values, indicating strong photosynthetic capacity. HBWF has a greater SLA and the highest LDMC but has the lowest LTD, WUE, and EWT, indicating that this provenance is water-intensive and high-yielding, with strong resource acquisition capability but poor drought stress resistance.

Research showed that variation in plant leaf functional traits is not only related to genetic diversity but also influenced by habitat heterogeneity [67,69]. Environmental factors at provenances location can significantly affect the variation in the leaf functional traits of Chinese fir provenances. After long-term geographical isolation and natural selection, different provenances of Chinese fir have formed, with nearly one-third of the variation still explained by the hydrothermal conditions of the location of provenances even after they were transplanted into a homogeneous garden environment [67,68].

4.3. Correlations among leaf functional traits

As shown in Figure 3, correlations among traits across the upper, middle, and lower canopy layers differ, reflecting the ecological strategies by which plant leaves adapt to varying environmental factors [14,17], such as light and moisture, at different canopy heights [25,26].

The synergistic associations among leaf functional traits indicate the survival strategies of plants [4]. Research has revealed a significant negative correlation between SLA and EWT, which reflects a plant's ability to capture light resources and manage water status [70], respectively. In subtropical regions characterized by intense sunlight and rapid evaporation, plants tend to allocate more dry matter to guard cells [59], resulting in a reduced SLA and increased leaf thickness or density. This adaptation fosters efficient water storage. The SPAD values were positively correlated with the WUE, LCC, and C:N ratios. Since SPAD values reflect a plant's photosynthetic capacity, Chinese fir, which has high photosynthetic ability, assimilates more carbon dioxide through photosynthesis while regulating stomatal conductance to minimize water loss, which enhances its WUE. Furthermore, more carbon is allocated to leaf tissue construction, resulting in a higher nitrogen utilization rate [71], which is consistent with previous research. In this study, we found that the correlations of leaf functional traits in the middle canopy layer were similar to the entire canopy (Figure 3), further confirming the feasibility of collecting samples from middle canopy leaves to examine the variation patterns of functional traits in subtropical *Cunninghamia lanceolata* forests.

4.4. Implications

In this study, we collected leaf samples from various geographical provenances of Chinese fir at different canopy heights and measured relevant functional traits. These findings confirm that the impact of canopy height on leaf functional traits of Chinese fir artificial forest is limited. This limitation is due primarily to the leaf shapes and canopy structures in Chinese fir forests [53], which allow some leaves in the middle and lower canopies to receive adequate light. However, significant intraspecific variation in functional traits is evident, and is influenced by genetic information [68]. Notably, some functional traits exhibited minor differences among provenances, which diverges from the findings of previous studies. The age of the leaves and their position on the branches (which determines the distance of water transmission) all affect the photosynthetic capacity of the leaves, which also have influence on functional traits. What's more, in this study, we focus on the variation of functional traits among provenances, but we only collect samples from only 3 specimens, which may affect the results. Future studies should increase the sample size to investigate the patterns of intraspecific variation.

Additionally, this study revealed that leaf samples from the middle canopy can effectively represent the overall functional traits of Chinese fir communities. Regardless of whether single trait values or the relationships among multiple traits are considered, the differences are minimal compared with the overall average values across different canopy heights. These findings have significant implications for understanding the ecological functions of Chinese fir artificial forests in subtropical regions.

5. Conclusions

.The variation in canopy height has a minor effect on Chinese fir leaf functional traits, with most of the functional traits variation attributed to the differences of provenances. Overall, 50% of the leaf functional traits presented significant correlations, which were associated mainly with photosynthetic capacity-related traits. The correlations among traits at the middle part of the canopy are consistent with the average canopy values. These results provide useful insights about adaptation of functional traits of Chinese fir to canopy microenvironment.

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Authorship contributes

Tingyu Xu: Conceptualization, Data curation, Formal analysis, Writing-original draft, Writing-review & editing. Xiang Niu: Conceptualization, Investigation, Writing-review & editing. Bing Wang: Investigation, Project administration. Yihui Wang: Data curation.

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Data availability

Availability of data and materials: The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declaration

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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References

1. Pérez-Ramos, I.M., Matías, L., Gómez-Aparicio, L. et al. Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. *Nat. Commun.*, 10, 2555 (2019). <https://doi.org/10.1038/s41467-019-10453-0>.
2. Gabriele, M., Pieter, D. F., Norbert H., et al. Global patterns of intraspecific leaf trait responses to elevation. *Glob. Chang. Biol.*, 25, 6 (2019). <https://doi.org/10.1111/gcb.14646>.
3. Li, Q., Wen, J., Zhao, C. Z., et al. The relationship between the main leaf traits and photosynthetic physiological characteristics of *Phragmites australis* under different habitats of a salt marsh in Qinwangchuan, China. *AoB Plants.*, 14, 6(2022). <https://doi.org/10.1093/aobpla/plac054>.
4. Wright, I.J., Reich, P.B., Westoby, M., et al. The world-wide leaf economics spectrum. *Nature*, 428, 821-827, (2004). <https://doi.org/10.1038/nature02403>.
5. Chave, J., Coomes, D., Jansen, S., et al. Towards a worldwide wood economics spectrum. *Ecol. Lett.*, 12(4): 351–366(2009). <https://doi.org/10.1111/j.1461-0248.2009.01285.x>.
6. E-Vojtkó, A., Junker, R.R., de Bello, F., et al. Floral and reproductive traits are an independent dimension within the plant economic spectrum of temperate central Europe. *New Phytol.* 236, 1964-1975(2022). <https://doi.org/10.1111/nph.18386>
7. Kleyer, M., Minden, V. Why functional ecology should consider all plant organs: An allocation-based perspective. *Basic Appl. Ecol.*, 16, 1-9(2015). <https://doi.org/10.1016/j.baec.2014.11.002>.
8. Liu, R., Yang, X. J., Gao, R. R., et al. Coordination of economics spectra in leaf, stem and root within the genus *Artemisia* along a large environmental gradient in China. *Glob. Ecol. Biogeog.*, 00, 1-15(2022). <https://doi.org/10.1111/geb.13624>.
9. Reich, P. B. The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *J. Ecol.*, 102(2): 275-301(2014). <https://doi.org/10.1111/1365-2745.12211>.
10. Li, J. L., Chen, X. P., Niklas, K. J., et al. A whole-plant economics spectrum including bark functional traits for 59 subtropical woody plant species. *J. Ecol.*, 110, 248-261(2022).
11. Zhao, Y. T., Ali, A., Yan, E. R. The plant economics spectrum is structured by leaf habits and growth forms across subtropical species. *Tree Physiology*, 37, 173-185(2016). <https://doi.org/10.1093/treephys/tpw098>.
12. Kramp, R. E., Liancourt, P., Hernerich, M. H., et al. Functional traits and their plasticity shift from tolerant to avoidant under extreme drought. *Ecology*, 103(12), e3826(2022). <https://doi.org/10.1002/ecy.3826>.
13. Vendramini, F., Diaz, S., Gurvich, D. E., et al. Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytol.*, 154, 1 (2002). <https://doi.org/10.1046/j.1469-8137.2002.00357.x>.
14. Wang, N., Lv, T., Wang, L. et al. Leaf functional traits and ecological strategies of common plant species in evergreen broad-leaved forests on Huangshan Mountain. *J. For. Res.* 35, 130 (2024). <https://doi.org/10.1007/s11676-024-01780-0>.
15. Liu, X. J., Ma, K. P. Plant Functional Traits—Concepts, Applications and Future Directions. *Scientia Sinica Vitae.*, 45, 4 (2015). <https://doi.org/10.1360/N052014-00244>.
16. Daniel, C. B. Unifying functional and population ecology to test the adaptive value of traits. *Biol. Rev.*, (2024). <https://doi.org/10.1111/brev.13107>.

17. Yu, H., Chen, Y., Zhou, G. et al. Coordination of leaf functional traits under climatic warming in an arid ecosystem. *BMC Plant Biol.*, 22, 439 (2022). <https://doi.org/10.1186/s12870-022-03818-z>.
18. Zhang, S. H., Zhang, Y., Xiong, K. N., et al. Changes of leaf functional traits in karst rocky desertification ecological environment and the driving factors. *Glob. Ecol. Conserv.*, 24(2020). <https://doi.org/10.1016/j.gecco.2020.e01381>.
19. Deng, F. Y., Xiao, L. Y., Huang, J., et al. Changes in leaf functional traits driven by environmental filtration in different monsoon tropical forest types. *Forests.*, 14, 10(2023) <https://doi.org/10.3390/f14102101>.
20. Sandra, D., Jens, K., Johannes, H. C. C., et al. The global spectrum of plant form and function: enhanced species-level trait dataset. *Sci. Data.*, 9, 475 (2022). <https://doi.org/10.1038/s41597-022-01774-9>.
21. Li, Y., Liu, C. C., Xu, L., et al. Leaf trait networks based on global data: Representing variation and adaptation in plants. *Front. Plant Sci.*, 12(2021). <https://doi.org/10.3389/fpls.2021.710530>.
22. Andrea, C. W., Carol, C. H. et al. Photosynthetic rates influence the population dynamics of understory herbs in stochastic light environments. *Ecology*, 98, 2(2016). <https://doi.org/10.1002/ecy.1664>.
23. Christopher H. L. Leaf functional trait variation in a humid temperate forest, and relationships with juvenile tree light requirements. *PeerJ*, 7:e6855(2019). <https://doi.org/10.7717/peerj.6855>.
24. Bigelow, S. W. Leaf nutrients in relation to stature and life form in tropical rain forest. *J. Veget. Sci.*, 4, 3(1993). <https://doi.org/10.2307/3235599>.
25. Aaron, G. K., Kyla, M. D., Shawn, P. S., et al. Leaf traits and canopy structure together explain canopy functional diversity: an airborne remote sensing approach. *Ecol. Appl.*, 31, 2(2020). <https://doi.org/10.1002/eap.2230>.
26. Duan, M. C., Li, L., Ding, G. G., et al. Leading nutrient foraging strategies shaping by root system characteristics along the elevations in rubber (*Hevea brasiliensis*) plantations. *Tree Physiol.* 42, (2022). <https://doi.org/10.1093/treephys/tpac081>.
27. Zuleta, D., MullerLandau, H. C., Duque, A., et al. Interspecific and intraspecific variation of tree branch, leaf and stomatal traits in relation to topography in an aseasonal Amazon forest. *Funct. Ecol.* 36, 2955-2968(2022). <https://doi.org/10.1111/1365-2435.14199>.
28. Poorter, H., Niinemets, U., Poorter, L., et al. Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytol.*, 182, 565-588(2009). <https://doi.org/10.1111/j.1469-8137.2009.02830.x>.
29. Ye, X., Bu, W. S., Hu, X. F., et al. Species divergence in seedling leaf traits and tree growth response to nitrogen and phosphorus additions in an evergreen broadleaved forest of subtropical China. *J. For. Res.*, 34, 137-150(2023). <https://doi.org/10.1007/s11676-021-01437-2>.
30. Yao, L. J., Xu, Y., Wu, C. P., et al. Variation in the functional traits of forest vegetation along compound habitat gradients in different climatic zones in China. *Forests*, 14, 6(2023). <https://doi.org/10.3390/f14061232>.
31. Zhang, Z. J., Wang, X., Guo, S. Q., et al. Divergent patterns and drivers of leaf functional traits of *Robinia pseudoacacia* and *Pinus tabulaeformis* plantations along a precipitation gradient in the Loess plateau, China. *J. Environ. Manag.*, 348, 119318(2023). <https://doi.org/10.1016/j.jenvman.2023.119318>.
32. Jana, D., Jan, D. Along with intraspecific functional trait variation, individual performance is key to resolving community assembly processes. *Funct. Ecol.*, 34, 11(2020). <https://doi.org/10.1111/1365-2435.13646>.
33. Facundo X. P., Gustavo J. F., Mariano, O. Does accounting for within-individual trait variation matter for measuring functional diversity? *Ecol. Indic.*, 102, 43-50(2019). <https://doi.org/10.1016/j.ecolind.2019.02.018>.
34. Olivia, L. C., Richard, L. L., Andrew H., et al. Trait plasticity and trade-offs shape intra-specific variation in competitive response in a foundation tree species. *New Phytol.*, 230, 2(2020). <https://doi.org/10.1111/nph.17166>.
35. Florian, H., Eduardo, C., Åke, B. Mechanisms driving plant functional trait variation in a tropical forest. *Ecol. Evol.*, 11, 9(2021). <https://doi.org/10.1002/ece3.7256>.
36. Albert, C. H., Thuiller, W., Yoccoz, N.G., et al. A multi-trait approach reveals the structure and the relative importance of intra-vs. Interspecific variability in plant traits. *Funct. Ecol.*, 24, 6(2010). <https://doi.org/10.1111/j.1365-2435.2010.01727.x>.
37. Siefert, A., Violle, C., Chalmandrier, L. et al. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecol. Lett.*, 18, 12(2015). <https://doi.org/10.1111/ele.12508>.
38. Laughlin, D. C. Applying trait- based models to achieve functional targets for theory- driven ecological restoration. *Ecol. Lett.*, 18, 12(2014). <https://doi.org/10.1111/ele.12288>.
39. Niemczyk, M., Chmura, D.J., Socha, J. et al. How geographic and climatic factors affect the adaptation of Douglas-fir provenances to the temperate continental climate zone in Europe. *Eur J Forest Res* 140, 1341 – 1361 (2021). <https://doi.org/10.1007/s10342-021-01398-5>.
40. Klisz, M., Buras, A., Sass-Klaassen, U., et al. Limitations at the limit? Diminishing of genetic effects in Norway spruce provenance trials. *Front. Plant Sci.* 10, 306(2019a). <https://doi.org/10.3389/fpls.2019.00306>.

41. Hevia, A., Campelo, F., Chambel, R., et al. Which matters more for wood traits in *Pinus halepensis* Mill., provenance or climate? *Annals of Forest Science* 77, 1 – 24(2020). <https://doi.org/10.1007/s13595-020-00956-y>.
42. Mihai, G., Teodosiu, M., Birsan, M.-V., et al. Impact of Climate Change and Adaptive Genetic Potential of Norway Spruce at the South—eastern Range of Species Distribution. *Agric. For. Meteorol.* 291, 108040(2020). <https://doi.org/10.1016/j.agrformet.2020.108040>.
43. Fei Y, Wu Q, Zhang X, et al. Effects of different undergrowth vegetation management measures on soil characteristics and timber outturn of *Cunninghamia lanceolata* large-diameter timber cultivation plantation. *Chin J Appl Environ Biol.* 2020. <https://doi.org/10.19675/j.cnki.1006-687x.2019.8011>.
44. State Forestry and Grassland Administration of China. (2019). China Forest resources report (2014 – 2018). Beijing: China Forestry Press.
45. Hong, J., Li, X., Chen, Y. Memoir of Chinese fir provenance test (in Chinese). *Forest Research.*, 7, 1994.
46. Cornelissen, J. H. C., Lavore, S., Garnier E., et al. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51, 335-380(2003). <https://doi.org/10.1071/bt02124>.
47. Pérez-Harguindeguy, N., Diaz, S., Garnier, E., et al. New handbook for the standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61(3), 167-234(2013). <https://doi.org/10.1071/BT12225>.
48. Farquhar, G. D., Richards, R. A. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Australian Journal of Plant Physiology*, 11, 539-552(1984). <https://doi.org/10.1071/PP9840539>.
49. Feng, J. Y., Lian, J. Y., Mei, Q. M., et al. Vertical variation in leaf traits and crown structure promote the coexistence of forest tree species. *Forests*, 13, 1548(2022). <https://doi.org/10.3390/f13101548>.
50. Jin, N., Yu, X. C., Dong, J. L., et al. Vertical variation in leaf functional traits of *Parashorea chinensis* with different canopy layers. *Frot. Plant Sci.*, 15, 1335524(2024). <https://doi.org/10.3389/fpls.2024.1335524>.
51. Adam, P. C., Marilyn, L. F., Geoffrey, G. P. Canopy gradients in leaf functional traits for species that differ in growth strategies and shade tolerance. *Tree Physiol.*, 37, 10, 1415-1425(2017). <https://doi.org/10.1093/treephys/tpx048>.
52. Liu, X. Q., Feng, Y. H., Hu, T. Y., et al. Enhancing ecosystem productivity and stability with increasing canopy structural complexity in global forests. *Sci. Adv.*, 10, ead1947(2024). <https://doi.org/10.1126/sciadv.adl1947>.
53. Wu, Q. L., Song, C. H., Song, J. L., et al. Effects of leaf age and canopy structure on gross ecosystem production in a subtropical evergreen Chinese fir forest. *Agri. For. Meteorol.*, 310, 108618(2021). <https://doi.org/10.1016/j.agrformet.2021.108618>.
54. Xian, W. F. Study on photosynthetic physiology and ecology simulation of canopy in Chinese fir plantation(1994). Chinese Academy of Forestry, Beijing.
55. Shen, T., Corlett, R. T., Collart, F., et al. Microclimatic variation in tropical canopies: A glimpse into the processes of community assembly in epiphytic bryophyte communities. *J. Ecol.* 110, 3023 – 3038(2022). <https://doi.org/10.1111/1365-2745.14011>.
56. Wright, S. J., Kitajima, K., Kraft, N. J. B., et al. Functional traits and the growth-mortality trade-off in tropical trees. *Ecol. Lett.*, 91, 12, 3664-3674(2010). <https://doi.org/10.2307/29779549>.
57. Petter, G. Wagner, K., Wanek, W., et al. Functional leaf traits of vascular epiphytes: Vertical trends within the forest, intra- and interspecific trait variability, and taxonomic signals. *Func. Ecol.*, 30, 188-198(2015). <https://doi.org/10.1111/1365-2435.12490>.
57. Burton, J. I., Perakis, S. S., McKenzie, S. C., et al. Intraspecific variability and reaction norms of forest understory plant species traits. *Func. Ecol.*, 31, 10, 1881-1893(2017). <https://doi.org/10.1111/1365-2435.12898>.
58. Wang, Q. W., Robson, T. M., Pieriste, M., et al. Testing trait plasticity over the range of spectral composition of sunlight in forb species differing in shade tolerance. *J. Ecol.*, 108, 5(2020). <https://doi.org/10.1111/1365-2745.13384>.
59. Kenzo, T., Inoue, Y., Yoshimura, M. et al. Height-related changes in leaf photosynthetic traits in diverse Bornean tropical rain forest trees. *Oecologia*, 177(1), 191-202(2015). <https://doi.org/10.1007/s00442-014-3126-0>.
60. Sonia, P.D., Marcin, K. D., Kinga, N, et al. On the sunny side of the crown-quantification of intra-canopy SLA variation among 179 taxa. *For. Ecol. Manag.*, 472, 118254(2020). <https://doi.org/10.1016/j.foreco.2020.118254>.
61. He, D., Yan, E.R. Size-dependent variations in individual traits and trait scaling relationships within a shade-tolerant evergreen tree species. *Am. J. Bot.*, 105(7):1165-1174(2018). <https://doi.org/10.1002/ajb2.1132>.
62. Jiang, Y. Variations in leaf traits with plant size and leaf height in karst forest trees(2022). Guizhou Normal University, Guizhou.
63. Tian, J. X., Wei, L. P., He, N. P., et al. Vertical variation of leaf functional traits in temperate forest canopies in China. *Acta Ecologica Sinica*, 38(23):8383-8391(2018). <https://doi.org/10.5846/stxb201801020006>.
64. Kunstler, G., Falster, D., Coomes, D. A., et al. Plant functional traits have globally consistent effects on competition.

- Nature, 529(7585):204-207(2016). <https://doi.org/10.1038/nature16476>.
65. Song, L. Y., Peng, C. L., Peng, S. L. Comparison of leaf construction costs between three invasive species and three native species in South China. *Bio. Sci.*, 17(4):378-384(2009). <https://doi.org/10.3724/SP.J.1003.2009.09077>
66. Tang, S. B., Zhang, L. L., Lambers, H., et al. Addition of nitrogen to canopy versus understorey has different effects on leaf traits of understorey plants in a subtropical evergreen broad-leaved forest. *J. Ecol.*, 109(2), 692-702. <https://doi.org/10.1111/1365-2745.13496>.
67. Xu, T. Y., Niu, X., Wang, B., et al. Variations in leaf functional traits and photosynthetic parameters of *Cunninghamia lanceolata* Provenances. *Forests*, 14, 1708(2023). <https://doi.org/10.3390/f14091708>.
68. Xu, R., Cheng, S., Zhou, J., et al. Intraspecific variations in leaf functional traits of *Cunninghamia lanceolata* provenances. *BMC Plant Biol.* 2023, 23, 92. <https://doi.org/10.1186/s12870-023-04097-y>.
69. Dong, X. X., Shi, L., Bao, S. Q., et al. Leaf traits of prickly ash and its correlation with ecological and geographical factors of origin. *Sci. Rep.*, 14, 1, 6276(2024). <https://doi.org/10.1038/s41598-024-56962-x>.
70. Luo, T., Yu, F. Y., Lian, J. Y., et al. Impact of canopy vertical height on leaf functional traits in a lower subtropical evergreen broad-leaved forest of Dinghushan (in Chinese). *Biodi. Sci.*, 30, 21414(2022).
71. Yue, K., Li, L., Fudjoe, S. K., et al. Nitrogen supply affects grain yield by regulating antioxidant enzyme activity and photosynthetic capacity of maize plant in the loess plateau. *Agronomy*, 11, 1094(2021). <https://doi.org/10.3390/agronomy11061094>.