

Article

Growth Rate and Leaf Functional Traits of Four Broad-Leaved Species Underplanted in Chinese Fir Plantations with Different Tree Density Levels

Rui Xu ¹, Liyan Wang ¹, Jian Zhang ¹, Jing Zhou ¹, Shundan Cheng ¹, Mulualet Tigabu ^{1,2} , Xiangqing Ma ^{1,3}, Pengfei Wu ^{1,3} and Ming Li ^{1,3,*}

- ¹ Forestry College, Fujian Agriculture and Forestry University, Fuzhou 350002, China; xurui6611@163.com (R.X.); wlyfafu@163.com (L.W.); z1z2j1j2@163.com (J.Z.); zj3023602668@163.com (J.Z.); cheng18050265870@163.com (S.C.); mulualet.tigabu@slu.se (M.T.); lxmymxq@126.com (X.M.); fjwupengfei@fafu.edu.cn (P.W.)
- ² Southern Swedish Forest Research Center, Faculty of Forest Science, Swedish University of Agricultural Sciences, P.O. Box 49, SE-230 53 Alnarp, Sweden
- ³ Chinese Fir Engineering Technology Research Center of National Forestry and Grassland Administration, Fuzhou 350002, China
- * Correspondence: limingly@126.com; Tel.: +86-18350068286

Abstract: The close-to-Nature management method of interplanting broad-leaved trees after thinning of monoculture plantations is an important mixed species restoration model to improve the ecological service and functions effectively as well as to reduce the productivity decline of the multi-generation continuous planting of monoculture. Thus, the selection of tree species for establishing mixed forest and its ecological adaptability are the key issues. In this study, we conducted thinning experiment in an 11-year-old Chinese fir plantation with retention density of 900 trees/ha, 1200 trees/ha and 1875 trees/ha, and then underplanted four broad-leaved species, *Schima superba*, *Phoebe bournei*, *Tsoongiodendron odorum* and *Michelia macclurei*. After three years, we analyzed the growth rate and leaf functional traits of the broad-leaved species and their correlations with stand characteristics. The results showed that growth rate of seedlings of the four broad-leaved species were significantly different ($p < 0.05$) among different tree density levels and species. Low tree density favored seedling growth compared with high tree density and seedlings of *T. odorum* and *S. superba* performed best. However, leaf functional traits varied significantly ($p < 0.01$) among species only, and *T. odorum* had the largest specific leaf area, the smallest leaf mass per unit area, the smallest leaf tissue density, relatively large leaf thickness, and relatively small dry matter content. The leaf C content varied significantly among tree density levels and species; leaf N content varied significantly among species only; and leaf *p* content varied among tree density levels only. Correlation analyses between growth characters and leaf functional traits showed that height growth was significantly correlated with leaf N content ($r = 0.686$; $p = 0.041$) and with C:N ratio ($r = -0.682$; $p = 0.043$). Root collar diameter growth was significantly correlated with specific leaf area ($r = 0.820$; $p = 0.007$), leaf N content ($r = 0.685$; $p = 0.042$), leaf thickness ($r = -0.706$; $p = 0.034$) and leaf mass per unit area ($r = -0.812$; $p = 0.008$). Thus, leaf functional traits possibly predict diameter growth better than height growth. As a whole, growth rate and leaf functional traits could be used as a guide for selection of species for under planting in thinned pure monoculture plantations to establish conifer-broadleaved mixed forests. Based on growth rate and leaf functional traits, *T. odorum* appeared to be suitable for planting under low tree density stands where the degree of shading is low.

Keywords: *Cunninghamia lanceolata*; mixed-species forest; leaf nutrient content; specific leaf area; stand attributes



Citation: Xu, R.; Wang, L.; Zhang, J.; Zhou, J.; Cheng, S.; Tigabu, M.; Ma, X.; Wu, P.; Li, M. Growth Rate and Leaf Functional Traits of Four Broad-Leaved Species Underplanted in Chinese Fir Plantations with Different Tree Density Levels. *Forests* **2022**, *13*, 308. <https://doi.org/10.3390/f13020308>

Academic Editor: Ilona Mészáros

Received: 30 December 2021

Accepted: 11 February 2022

Published: 14 February 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Restoration of mixed species forests has gained increasing recognition as a strategy to spread the risks associated with predicated climate changes that will alter precipitation regimes and a rise in air temperature in the next hundred years and provision of several ecosystem services [1]. The close-to-nature management method of under planting broad-leaved trees after thinning of the middle-aged monoculture plantation is opined to be an important mixed-species forest restoration model to effectively improve the ecological services and reduce the productivity decline of the multi-generation continuous planting of monoculture plantation. Reasonable thinning plays a vital role in forest management as it improves the growing space of the forest canopy and the supply of nutrients and groundwater for individual trees, thus resulting in increased production of the forests [2,3]. This management model also promotes nutrient cycling, and improves soil fertility and the diversity of soil microorganisms through diversified litter fall [4]. In recent years, forest management in China has shown that planting broad-leaved tree species in the understory of coniferous forests to create a mixed coniferous–broad-leaved multi-layered forest structure is an effective production and management model to promote the vicious cycle of the artificial forest establishment [5,6]. Using existing growth models, mixed forests are shown to be more suitable for certain sites and climatic conditions [7] and may circumvent the down sides of monocultures, such as decline of forest production through successive plantation of monocultures on the same place and decline of soil nutrient availability [8].

Under the close-to-Nature management model, choosing the broad-leaved trees suitable for under planting at an appropriate thinning retention density is a key issue. Thus, an efficient approach to species selection for establishment of mixed-species forest is necessary, and trait-based approach could be one option to achieve success in restoration of mixed-species forests by converting monoculture plantations, such as pure plantation of Chinese fir, into mixed species stands by under planting appropriate broad-leaved species. Species differ in many functional traits that drive changes in photosynthetic rates, biomass allocation, and tissue turnover. Plant functional traits is a series of core plant attributes about the life cycle of the plant body [9], which can reflect the adaptations of plants to environmental change and trade-offs, and thus can better link environmental drivers and plant responses to ecosystem structure and functioning [10]. A suite of plant functional traits has been suggested to be of significance importance in understanding plant regeneration and performance [11–13]. Among plant functional traits, leaf traits (specific leaf area, leaf mass per unit area, leaf dry matter content, leaf density, and leaf thickness) denotes trade-off between strategic allocations to construction costs [14], photosynthetic rate, and leaf life spans [15,16]. Leaves have the largest contact area with the external environment and are most sensitive to environmental changes. They are also the main organ of plants for photosynthesis and material production; thus directly affect the basic functions of plants and best reflect the adaptability of plants [7]. For instance, physiological performance, especially photosynthetic rate (P_n) and stomatal conductance (G_s), increases with higher specific leaf weight, higher contents of chlorophyll and nitrogen, and thicker leaves that help capturing more light that will convert light energy into chemical energy [17,18].

Leaf morphological traits are also good indicators of plant acclimation potential and adaptation to light conditions (light demanding versus shade tolerant). Shade tolerant species have high specific leaf area (SLA) whereas light-demanding species are characterized by a low SLA and nitrogen concentration, which in turn lead to high photosynthesis, respiration, and conductance rates [16]. Thus, SLA is a good indicator of the trade-off between resource capture [8]. It also links plant carbon (C) and water cycles, and can reflect changes in leaf photosynthetic capacity and nitrogen (N) content [19]. Leaf dry matter content (LDMC) is a predictor of the ability of plant leaves to capture and use light resources under shading conditions, thereby optimizing photosynthetic efficiency under low light availability [20], and increases growth rate and C assimilation [21]. Leaf tissue density reflects the carrying capacity and defense capability of plants against biological

factors, and it is closely interrelated to the leaf growth rate [22]. Leaf mass per unit area has also been shown to be associated with shading; i.e., reduction in leaf mass per unit area with increasing shading [23]. Thus, leaf mass per unit area could be considered a species-specific estimate of long-term light conditions. Leaf N and phosphorus (P) contents, and leaf thickness (LT) are also important indicators of leaf functional traits, as they are closely related to SLA and LDMC [24]. The amount of N and P contents in plants reflect nutrient uptake, utilization efficiency and adaptation to the environmental stress. Higher N contents are associated with higher leaf area index values, extended photosynthesis duration and greater nutrient uptake [25]. Phosphorus influences photosynthetic assimilation and biomass production in plants [25]. Studies have also shown that plants growing under shading conditions will have increased leaf N content and allocate more N to increase chlorophyll content to prevent photo-damage and enhance light use efficiency and keep normal photosynthetic function [26].

Currently, converting Chinese fir monoculture plantations into conifer-broadleaved forest is actively pursued in southern China through planting of one kind of broad-leaved species in different tree densities of Chinese fir plantations or growing several kinds of broad-leaved species planted in different places in the same tree density of Chinese fir plantations. However, there is a lack of comparative experiments on simultaneous under planting of multiple broad-leaved tree species in Chinese fir plantations under different thinning retention densities. In addition, the selection of broadleaved species is not based on scientific evidence. Here we hypothesized that (1) the planted species differ in growth rate in response to tree density of Chinese fir plantations; (2) leaf functional traits vary among species in response to tree density; (3) there is a relationship between growth rate and leaf functional traits; and (4) leaf functional traits could be good predictor of growth of broadleaved species planted under different tree density levels. Therefore, we set up an experiment involving under planting of four broad-leaved tree species, *Schima superba* Gardner & Champ., *Phoebe bournei* (Hemsl.) Yen C. Yang, *Tsoongiodendron odorum* Chun and *Michelia macclurei* Dandy, in Chinese fir plantations with three tree density levels (900, 1200 and 1850 trees/ha). We recorded annually seedling height and root collar diameter for three consecutive years and five leaf morphological traits (leaf thickness, specific leaf area, leaf mass per unit area, leaf dry matter content and leaf tissue density) and three leaf biochemical traits (carbon, Nitrogen and phosphorus contents) and their ratio (C:N, C:P and N:P). The main objective of this study was to identify species suitable for under planting in different tree density levels of Chinese fir monoculture plantations based on growth rate and leaf functional traits. Specifically, we compared growth rate of seedlings of the broad-leaved species under different tree density levels, examined variations in leaf functional traits among species under different tree density levels and related the functional traits with growth rate.

2. Materials and Methods

2.1. Study Site

The study site is located at 26°50' N, 117°54' E in Shunchang State-owned Forest Farm, Fujian Province, which is a low hilly branch of the Wuyi Mountain. It belongs to the mid-subtropical maritime monsoon climate zone—the central production area of Chinese fir. The average annual temperature is 18.5 °C, the average annual precipitation is 1880.2 mm, and the frost-free period is 280 d. The stand site index is 22, the altitude is 300–800 m, and the average slope is 31°. The soil is mainly mountain red soil, with uniformly low phosphorus content across the 0–40 cm soil depth. The soil physical and chemical properties of the stands are given in Table 1.

Table 1. Soil physical and chemical properties and stand characteristics of Chinese fir stands (mean \pm SE, $n = 3$).

Soil Depth (cm)	Soil Physico-Chemical Properties and Stand Characteristics	Tree Density/ha		
		1875	1200	900
0–10	soil bulk density (g/cm ³)	1.14 \pm 0.12	1.1 \pm 0.09	1.2 \pm 0.09
	maximum water holding capacity (%)	514.6 \pm 100.2	494.8 \pm 77.0	433.9 \pm 26.7
	Minimum water holding capacity (%)	421.7 \pm 64.9	409.2 \pm 59.9	389.1 \pm 15.5
	total porosity (%)	57.4 \pm 6.3	53.7 \pm 4.3	51.7 \pm 0.9
	Carbon content	23.2 \pm 3.1	29.2 \pm 5.6	27.2 \pm 9.5
	Nitrogen content	1.1 \pm 0.1	1.3 \pm 0.2	1.4 \pm 0.5
	Phosphorus content	0.1 \pm 0.0	0.1 \pm 0.0	0.1 \pm 0.0
10–20	soil bulk density (g/cm ³)	1.23 \pm 0.12	1.19 \pm 0.03	1.28 \pm 0.11
	maximum water holding capacity (%)	411.7 \pm 58.8	435.3 \pm 39.4	388.3 \pm 49.5
	Minimum water holding capacity (%)	353.0 \pm 39.9	372.4 \pm 36.8	341.1 \pm 47.0
	total porosity (%)	49.8 \pm 2.8	51.8 \pm 3.1	49.3 \pm 2.1
	Carbon content	18.3 \pm 3.4	18.7 \pm 6.2	18.5 \pm 9.6
	Nitrogen content	0.9 \pm 0.1	0.8 \pm 0.1	0.8 \pm 0.2
	Phosphorus content	0.1 \pm 0.0	0.1 \pm 0.0	0.1 \pm 0.0
20–40	soil bulk density (g/cm ³)	1.38 \pm 0.03	1.34 \pm 0.05	1.36 \pm 0.04
	maximum water holding capacity (%)	329.4 \pm 15.6	332.4 \pm 36.4	345.2 \pm 17.3
	Minimum water holding capacity (%)	289.7 \pm 0.2	297.5 \pm 23.7	295.4 \pm 14.9
	total porosity (%)	45.4 \pm 1.7	44.4 \pm 3.6	46.8 \pm 1.0
	Carbon content (g/kg)	11.4 \pm 1.8	10.1 \pm 1.7	15.4 \pm 5.5
	Nitrogen content (g/kg)	0.6 \pm 0.1	0.5 \pm 0.1	0.7 \pm 0.2
	Phosphorus content (g/kg)	0.1 \pm 0.0	0.1 \pm 0.0	0.1 \pm 0.0
Stand characteristics				
	Leaf area index	2.36 \pm 0.15	2.58 \pm 0.70	2.01 \pm 0.65
	Non-intercepted scattering	0.17 \pm 0.02	0.17 \pm 0.09	0.24 \pm 0.11

In 2017, a thinning experiment was conducted in middle-aged Chinese fir plantations that were established 11 years ago, and the tree density was adjusted from 1850 trees/ha (no thinning) to 900 trees/ha and 1200 trees/ha. After thinning, three 20 \times 20 m standard plots were set up under each tree density treatment, and each density treatment was repeated three times, yielding a total of nine plots. Container-grown seedlings of four broad-leaved trees of two-year-old; *S. superba*, *P. bournei*, *T. odorum* and *M. macclurei*, were planted in each sample plot. In each plot, nine individuals of each species were planted, and a total of 36 broad-leaved trees in a plot were randomly distributed in the plantations. The species were chosen based on their economic and conservation values. *S. superba* is the main evergreen broad-leaved forest tree species in the subtropical region of China that can be used as a forest fire line tree and has high ecological value [19]. *P. bournei* is an endemic evergreen tree in China, which is the national second-level protected species. The timber, which is extremely precious, has some features, such as fragrance, beautiful texture, and more bright spots or golden threads on the section [21]. *M. macclurei* is a broad-leaved evergreen tree species, which is fast growing and best adaptable, and it is an excellent fire-resistant tree species [22]. *T. odorum* is a rare and endangered secondary protected species in China. It is also one of the precious native tree species advocated by Fujian Province, China [24]. They all have the advantages of straight trunks and dense crowns, so they are excellent timber tree species and ornamental tree species. In addition, these four tree species have some degree of shade-tolerance, and hence are well suited for planting in the understory environments.

2.2. Measurements of Growth and Leaf Functional Traits

From April to May each year, the height and root collar diameter of seedlings of broad-leaved species were measured. In September 2020, five leaves of each broad-leaved

tree in the sample plots were collected, and a total of 45 leaves were measured for each tree species in the sample plot. The leaf area (LA) was determined by scanning the leaves with a flatbed scanner and analyzing the images using area measurement software (Image J, National Institutes of Health, Bethesda, MD, USA). After weighing leaf saturated fresh mass, all leaf samples were oven-dried at 80 °C for 72 h to constant mass and weighed for their dry mass. The specific leaf area (SLA) was calculated for each leaf as the ratio of leaf area to leaf dry mass. Leaf mass per unit area (LMA) was computed as the ratio of leaf dry weight to leaf area. Leaf dry matter content (LDMC) was computed as the ratio of leaf dry mass to leaf saturated fresh mass. Leaf tissue density (LTD) was calculated for each leaf as the ratio of leaf dry weight to leaf volume [25,26]. LAI-2200C canopy analyzer (LI-COR Biosciences Ltd., Cambridge, UK) was used to measure leaf area index and non-intercepted scattering of the sample site. The leaf area index was 2.36, 2.58 and 2.01 for stands with 1850, 1200 and 900 trees/ha, respectively; and the non-intercepted scattering was 0.17 for stands with 1850 and 1200 trees/ha and 0.24 for the stand with 900 trees/ha (Table 1).

Leaf C, N and P contents were determined on dried leaf samples. All leaves from the same species at the same treatment were mixed into a single sample and grounded to 0.149 mm for chemical determination. Leaf C and N content were analyzed using Vario Max carbon and nitrogen element analyzer (Elementar, Frankfurt, Germany). Total leaf P content were measured by a molybdate/stannous chloride method after HNO₃-H₂O₂ digestion by ETHOS UP microwave digestion apparatus (Milestone, Milan, Italy). All nutrient analyses were replicated three times.

2.3. Data Analysis

Annual height and root collar diameter growth of planted seedlings were computed as the difference in 2018 and 2020 measurements divided by the time difference. To examine the effect of different tree density levels and trees species on growth rate and leaf functional traits, we conducted two-way analysis of variance (ANOVA), and significant differences were evaluated at $p < 0.05$ level. When significance was observed, the Duncan post hoc test was used to conduct multiple comparisons among treatments. All data were expressed as the mean \pm standard error (SE). Redundancy analysis (RDA) was used to examine the relationships between stand characteristics and growth and leaf functional traits. Prior to RDA, we conducted detrended canonical analysis (DCA) to see if RDA analysis is applicable. As the lengths of gradient was 1.291 which is shorter than 3.0, RDA was applicable. Finally, Pearson correlation analysis was used to test if leaf functional traits had predictive ability of seedling growth. Analysis of variance and correlation analyses were performed using the SPSS 22.0 software (SPSS, Chicago, IL, USA) while RDA was performed using Canoco (Version 5, Microcomputer Power, Ithaca, NY, USA).

3. Results

3.1. Growth Rate and Leaf Functional Traits

Annual growth rate in root collar diameter showed significant variation among different tree density levels whereas significant difference in annual height growth was observed both among tree density levels and species, but no interaction effects was observed (Table 2). Both height and root collar diameter growth was higher in low tree density stand than high tree density stand. Among species, height growth was higher for *T. odorum* and *S. superba* than *P. bournei*. On the contrary, leaf functional traits varied significantly among species but not among tree density levels and no significant interaction effects were observed (Table 3). Leaf thickness was low for *S. superba* followed by *P. bournei* compared with *T. odorum* and *M. macclurei*. Specific leaf area was higher while leaf mass per unit area was lower for *T. odorum* than other species. Leaf dry matter content was high for *P. bournei*, followed by *S. superba* and the least was for *T. odorum* and *M. macclurei*. Leaf tissue density was higher for *S. superba* and *P. bournei* than *T. odorum*.

Table 2. Annual growth rate of seedlings of four broad-leaved trees species underplanted in Chinese fir plantations with different tree density levels (Mean \pm SE). Means followed by different lower case letters are different among tree density levels and those followed by upper case letters are significantly different among species.

Tree Density/ha	Height (cm)	Diameter (cm)	Species	Height (cm)	Diameter (cm)
900	36.9 \pm 7.0 b	48.1 \pm 7.0 b	<i>T. odorum</i>	31.0 \pm 6.4 B	35.7 \pm 6.9 A
1200	27.3 \pm 3.0 b	35.7 \pm 3.0 ab	<i>S. superba</i>	32.2 \pm 6.1 B	44.3 \pm 7.5 A
1875	13.9 \pm 1.1 a	23.8 \pm 1.0 a	<i>P. bournei</i>	18.0 \pm 4.0 A	26.7 \pm 3.0 A
<i>p</i> -value	<0.001	0.002	<i>M. macclurei</i>	22.9 \pm 3.7 AB	36.8 \pm 4.0 A
			<i>p</i> -value	0.035	0.115

Table 3. Leaf functional traits of four broad-leaved trees species underplanted in Chinese fir plantations with different tree density (Mean \pm SE). Means followed by different lower case letters are different among tree density levels and those followed by upper case letters are significantly different among species.

Tree Density/ha	LT/mm	SLA/cm ² ·g ⁻¹	LMA/g·(cm ²) ⁻¹	LDMC/g·g ⁻¹	LTD/g·(cm ³) ⁻¹
900	0.17 \pm 0.01 a	169.3 \pm 12.3 a	0.006 \pm 0.0004 a	0.42 \pm 0.04 a	0.040 \pm 0.005 a
1200	0.16 \pm 0.01 a	172.8 \pm 11.8 a	0.006 \pm 0.0004 a	0.39 \pm 0.03 a	0.042 \pm 0.004 a
1875	0.14 \pm 0.01 a	199.9 \pm 17.9 a	0.005 \pm 0.0003 a	0.43 \pm 0.03 a	0.044 \pm 0.001 a
<i>p</i> -value	0.299	0.163	0.052	0.144	0.809
Species	LT/mm	SLA/cm ² ·g ⁻¹	LMA/g·(cm ²) ⁻¹	LDMC/g·g ⁻¹	LTD/g·(cm ³) ⁻¹
<i>T. odorum</i>	0.19 \pm 0.01 B	225.5 \pm 6.9 B	0.005 \pm 0.0001 A	0.35 \pm 0.02 A	0.024 \pm 0.001 A
<i>S. superba</i>	0.12 \pm 0.01 A	151.9 \pm 6.0 A	0.007 \pm 0.0003 B	0.41 \pm 0.01 B	0.059 \pm 0.006 C
<i>P. bournei</i>	0.14 \pm 0.02 AB	171.4 \pm 26.4 AB	0.007 \pm 0.0005 B	0.58 \pm 0.02 C	0.050 \pm 0.006 BC
<i>M. macclurei</i>	0.18 \pm 0.01 B	174.0 \pm 7.8 AB	0.006 \pm 0.0002 B	0.31 \pm 0.01 A	0.034 \pm 0.002 AB
<i>p</i> -value	0.008	0.007	<0.001	<0.001	<0.001

LT = leaf thickness, SLA = specific leaf area, LMA = leaf mass per unit area; LDMC = leaf dry matter content; and LTD = leaf tissue density.

The C, N and P contents of four broad-leaved species that were planted under Chinese fir stands differing in tree density are given in Table 4. The leaf C content varied significantly among tree density levels and species. It was higher in seedlings grown under both low and intermediate tree density than high tree density while *S. superba* and *P. bournei* had higher leaf C content than *T. odorum*. Leaf N content varied significantly among species only, while leaf P content varied among tree density levels only. *T. odorum* had higher N content than the other species and seedlings grown under high tree density had higher leaf P content than seedlings grown in low and intermediate tree density. The C:N ratio varied significantly among species only whereas the C:P and N:P ratio varied significantly among both species and tree density levels. The C:N ratio was lowest for *T. odorum* compared to other species; the C:P ratio was lowest for *T. odorum* and *P. bournei*; and the N:P ratio was lowest for *P. bournei* compared to other species. Seedlings grown under high tree density had lower C:P and N:P ratios than those grown under both low and intermediate tree density.

Table 4. C, N and P contents of four broad-leaved tree species underplanted in Chinese fir plantations with different tree density (Mean \pm SE). Means followed by different lower case letters are different among tree density levels and those followed by upper case letters are significantly different among species.

Tree Density/ha	C/g·kg ⁻¹	N/g·kg ⁻¹	P/g·kg ⁻¹	C:N	C:P	N:P
900	472.7 \pm 3.3 b	22.7 \pm 1.2 a	0.56 \pm 0.03 a	21.4 \pm 1.1 a	878.0 \pm 50.2 b	41.7 \pm 2.6 b
1200	473.5 \pm 2.6 b	23.2 \pm 1.2 a	0.56 \pm 0.03 a	21.0 \pm 1.1 a	870.8 \pm 49.8 b	41.6 \pm 1.4 b
1875	467.2 \pm 4.6 a	22.6 \pm 0.8 a	0.67 \pm 0.04 b	21.9 \pm 0.8 a	688.5 \pm 32.6 a	33.6 \pm 1.8 a
<i>p</i> -value	0.006	0.801	0.037	0.85	0.004	0.001
Species	C (g/kg)	N (g/kg)	P (g/kg)	C:N	C:P	N:P
<i>T. odorum</i>	453.9 \pm 3.2 A	28.2 \pm 0.9 B	0.66 \pm 0.04 A	16.2 \pm 0.5 A	709.7 \pm 45.7 A	43.7 \pm 2.6 B
<i>S. superba</i>	477.4 \pm 1.1 C	20.8 \pm 0.6 A	0.57 \pm 0.06 A	23.1 \pm 0.6 B	891.7 \pm 73.5 B	38.8 \pm 3.1 AB
<i>P. bournei</i>	482.7 \pm 1.5 C	20.8 \pm 0.5 A	0.64 \pm 0.03 A	23.3 \pm 0.6 B	770.5 \pm 38.0 A	33.1 \pm 1.3 A
<i>M. macclurei</i>	470.8 \pm 1.4 B	21.7 \pm 0.8 A	0.52 \pm 0.04 A	22.0 \pm 0.8 B	877.8 \pm 56.2 B	40.3 \pm 1.7 B
<i>p</i> -value	<0.001	<0.001	0.077	<0.001	0.032	0.003

3.2. Relationship between Stand Characteristics, Seedling Growth, and Leaf Functional Traits

Redundancy analysis was performed to examine the relationship between stand characteristics (tree density, leaf area index and non-intercepted scattering) and growth and leaf functional traits of four broad-leaved tree species (Figure 1). The results showed that except height growth of *M. macclurei*, height and root collar diameter growth rates of the species were significantly negatively correlated with tree density of Chinese fir plantation. There was negative correlations between the specific leaf area, leaf C and N contents, C:P and N:P ratios of *T. odorum* and tree density. Specific leaf area and leaf P content was positively correlated with leaf area index, but negatively correlated with non-intercepted scattering. For *S. superba*, tree density was positively correlated with leaf tissue density and C:N ratio while negatively correlated with leaf N content, and N:P ratio. Similarly, leaf thickness and leaf dry matter content showed positive correlation with non-intercepted scattering.

For *P. bournei*, non-intercepted scattering was positively correlated with leaf dry matter content, leaf tissue density, C content, C:P and N:P ratios; tree density was positively correlated with N content and specific leaf area. Leaf area index was positively correlated with P content. On the contrary, tree density was negatively correlated with leaf thickness, leaf mass per unit area and C:N ratio. The leaf tissue density of *M. macclurei* showed positive correlation with tree density, but tree density was negatively correlated with leaf thickness, C content, C:P and N:P ratios. Leaf tissue density and non-intercepted scattering had a positive correlation, and leaf N and P contents had positive correlation with leaf area index.

3.3. Correlations between Growth Characters and Leaf Functional Traits

Correlation analyses between growth characters and leaf functional traits were performed to examine whether the traits have prediction importance on seedling growth. The analysis showed that height growth was significantly positively correlated with leaf N content ($r = 0.686$; $p = 0.041$) but significantly negatively correlated with C:N ratio ($r = -0.682$; $p = 0.043$). Root collar diameter growth was significantly positively correlated with specific leaf area ($r = 0.820$; $p = 0.007$) and leaf N content ($r = 0.685$; $p = 0.042$), but significantly negatively correlated with leaf thickness ($r = -0.706$; $p = 0.034$) and leaf mass per unit area ($r = -0.812$; $p = 0.008$). The rest of the traits did not correlate significantly with height and diameter growth.

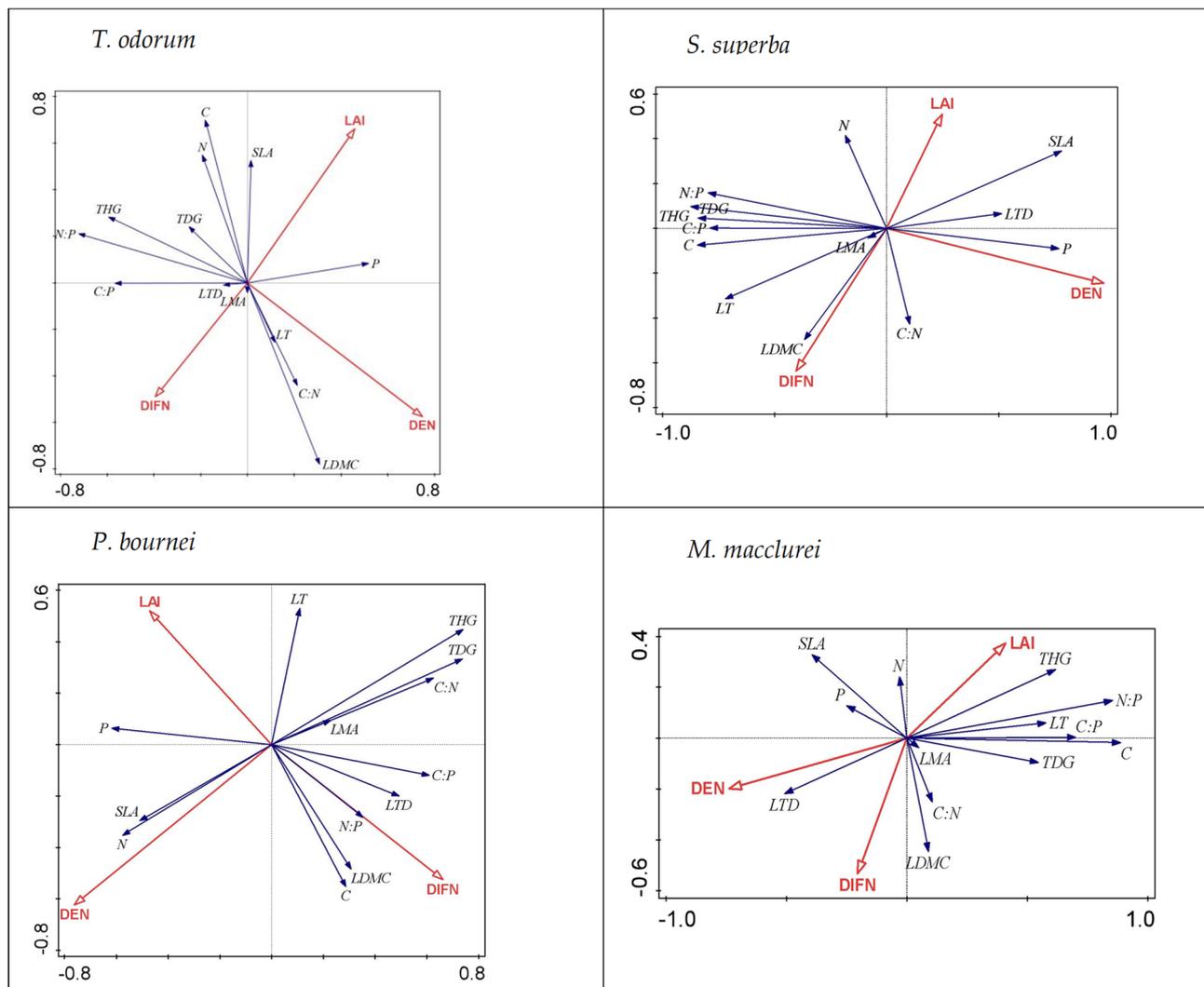


Figure 1. The RDA analysis of growth, leaf functional traits and C, N, P stoichiometry and environmental factors. Where LAI, DEN and DIFN stand for leaf area index, tree density and non-intercepted scattering, respectively. THG, TDG, SLA, LTD, LT, LMA, LDMC represent height growth, ground diameter growth, specific leaf area, leaf tissue density, leaf thickness, leaf mass per unit area, leaf dry matter content.

4. Discussion

Tree growth generally differs as a function of species, age, tree density, and site quality. Particularly, tree density influences tree growth as well as the structure and function of the forest ecosystem [27]. In this study, low tree density significantly increased the root collar diameter and height growth (Table 2). The increased tree growth with low tree density can be associated with reduced competition for growing resources, such as light, water and nutrients [28–31], which in turn influences crown size, photosynthetic rate and hormonal growth regulations [32]. Obviously a large number of trees in a high tree density stand compete for the same amount of belowground resources (nutrients and water) compared to low tree density stand [33]. Our results are consistent with previous studies that demonstrated a decrease in diameter growth with increasing tree density [34–36]. Our study also showed that height growth was generally higher in low and intermediate tree density than high tree density stand, with marked variation among species. *T. odorum* and *S. superba* seedlings grew faster in height than the other two species. Generally, the relation between tree density and height growth varies among sites, tree species and

stand growth. Previous studies have shown greater height growth in intermediate tree density than high tree density stand [37,38], which are in line with our results.

Tree density had no significant effect on leaf functional traits but significant inter-species variation was observed in leaf functional traits (Table 3). As all species planted in this study show some degree of shade tolerance [21,22,24,39], the effect of tree density appeared to be insignificant. Among the four-broadleaved species underplanted in Chinese fir stands, *T. odorum* had the largest leaf thickness and specific leaf area, but the smallest leaf mass per unit area, the smallest leaf tissue density, and the lowest dry matter content. Previous studies have shown that shade tolerant species have high SLA but lower leaf dry matter content (LDMC), which are predictors of the ability of plant leaves to capture and use light resources under shading conditions, thereby optimizing photosynthetic efficiency under low light availability [16,20,40,41]. Leaf tissue density relates to defense capability of plants against herbivores, and it is closely interrelated to the leaf growth rate [21]. Thus, *T. odorum* has better shade tolerance than the other species and likely susceptible to attack by herbivores under shade conditions. It has also been shown that specific leaf area and leaf dry matter content are negatively correlated [42]. This suggests that increased specific leaf area allows the species to absorb light that reach the understory efficiently, and hence have a better survival and growth. This is further evidenced in the present study where height growth of *T. odorum* was significantly higher than the other species. Leaf mass per unit area is the inverse ratio of specific leaf area, and its size is affected by leaf thickness and leaf tissue density. If a plant has larger leaf mass per unit area, it would mean that it has more dry matter accumulation per unit leaf area, and has stronger ability to tolerate low light environments. Previous studies have shown that the reduction in leaf mass per unit area with increasing shading could be considered as species-specific estimate of long-term light conditions [23]. As a whole, except for the leaf thickness of *P. bournei*, the other functional traits are opposite to those of *T. odorum*. This suggests that the under planting environment in the Chinese fir plantation is most suitable for the growth of *T. odorum* and the least suitable for the growth of *P. bournei*.

Both tree density and species influenced the C, N, and P contents (Table 4). Low and intermediate tree density resulted in higher leaf C content, C:P and N:P ratios than high tree density while the latter resulted in higher leaf P content. This difference could be related to belowground resource availability for increased uptake and better light availability that drives increased photosynthesis rate. Among species, *T. odorum* has the lowest leaf C content but the highest leaf N content, whereas *S. superba* and *P. bournei* had the highest leaf C content but the lowest N content. Shade-tolerant species, such as *S. superba*, have higher non-structural carbohydrate accumulation and C pool than shade-intolerant plants [39], mainly because their photosynthetic machinery is more efficient in the low light condition and store more C than shade-intolerant species. In addition, species growing under low light condition will have increased leaf N content and allocate more N to photosynthetic pigments, such as *T. odorum*. N is essential macro-element for plant growth and development, and involves in a number of metabolic processes. For instance, species use more N resources to synthesize light-trapping proteins (such as chlorophyll) under low light intensity [43]. Carbon is the main ingredient of carbohydrates, and it is the basis for growth, reproduction and structure of trees [44,45]; whereas P is the key component in the synthesis of genetic material [46]. The differences in leaf C and N contents among species could also be explained by the differences in growth rate among species. For instance, *T. odorum* grew faster in height than the other species; and this in turn requires consumption of a large amount of carbon to maintain the fast growth than accumulation in the leaf. The C:N ratio was the largest for *S. superba* and *P. bournei*; and C:P ratio was the largest for *S. superba* and *M. macclurei*, and the N:P ratio was the largest for *T. odorum* and *M. macclurei*. Thus, *T. odorum* has low N and P use efficiency while the other three species have better N and P use efficiency. It should be noted that the C: N and C:P ratios of plant leaves can reflect the utilization efficiency of N and P by plants [47,48], while N:P ratio reflects the restriction of N and P on plant growth and development [42].

Our findings showed significant correlations between stand characteristics and growth and functional traits (Figure 1). Tree density is the most important environmental condition that differs in this experiment, which has a greater impact on the growth of the four broad-leaved trees. The RDA results showed that height and root collar diameter growth of underplanted broad-leaved species, except height growth of *M. macclurei*, were negatively correlated with tree density. This indicates that nutrient availability in the stand with low tree density is adequate, and the competition between individuals is small, thus the growth rate is faster. The specific leaf area of *T. odorum* and tree density was negatively correlated, and the specific leaf area of *S. superba*, *P. bournei*, and *M. macclurei* were positively correlated with tree density. The large specific leaf area represents sufficient plant resource acquisition efficiency. Therefore, in stands with low tree density, *T. odorum* acquires more resources, while in the high tree density stand, the competitiveness of *T. odorum* was reduced. The leaf tissue density of *S. superba*, *P. bournei*, and *M. macclurei* were also positively correlated with tree density, while the leaf tissue density of *T. odorum* and tree density had not obvious correlation. Leaf tissue density represents the defense of the plant to biotic stresses; thus the defense ability of *S. superba*, *P. bournei*, and *M. macclurei* increases following an increase in tree density (excessive shading), where pathogens and herbivores are commonplace in moist and dense understory.

The leaf area index is another stand characteristic, which is the sum of the area of a single leaf of a plant per unit of surface area [49]. Non-intercepted scattering is also a key stand attribute that is not obscured by plant leaves [50]. These two stand characteristics reflect the light environment of the sites, and reflects the adaptation of plants to different light conditions. The non-intercepted scattering and leaf area index did not significantly affect the leaf functional traits of *S. superba*, suggesting that this species is shade tolerant as reported previously [51]. The height growth of *M. macclurei* had a positive correlation with non-intercepted scattering, suggesting that *M. macclurei* grows better in sufficiently light-rich environment. The content of P of *T. odorum* and the leaf area index was positively correlated; the C:P of the leaves of *P. bournei* was positively correlated with leaf area index; the C:N of the leaves of *M. macclurei* was positively correlated with the non-intercepted scattering; and the contents of N and P of leaves of *M. macclurei* were positively correlated with leaf area index. These results indicate that light has a greater impact on the utilization of N and P by the plants. The P utilization rate of *T. odorum* and *M. macclurei* are low in the condition of insufficient light, and the utilization of N by *M. macclurei* increases with increasing light level; thus, these two broad-leaved species are suitable for under planting in an environment with sufficient light availability. On the contrary, the P use efficiency of *P. bournei* is improved when the light availability is relatively weak; thus *P. bournei* is more shade-tolerant than other tree species [52].

The predictive ability of leaf functional traits for growth was examined by correlation analysis. We found that some leaf functional traits possibly predict diameter growth better than height growth. We observed that root collar diameter growth was significantly positively correlated with specific leaf area and leaf N content, but significantly negatively correlated with leaf thickness and leaf mass per unit area. It has been shown that low light induces carbohydrate deficiency, leading to slow growth [53,54]. As a result, plants store non-structural carbohydrates (NSCs), soluble sugar and starch content to enhance survival and growth under low light intensity [6,7,25,39]. Once the plant is exposed to low light intensity, the NSCs decreases, as the plants use their energy stores for growth and a decrease in C fixation [55]. Previous studies have shown that functional traits are weak predictors of juvenile tree growth at a global scale but are good predictor at local level [15,16,56]. In a study made on 24 species and 14 plant functional traits, it was found that nine traits were good predictors across all species [15]. Similarly, high leaf mass per area was found to be associated with root collar diameter growth under drought condition [57]. These studies supports our results that some leaf functional traits (e.g., specific leaf area and leaf N content) predicted root collar diameter of the studied species.

5. Conclusions

Annual growth rate and leaf functional traits of four broadleaved species (*T. odorum*, *M. macclurei*, *P. bournei* and *S. superba*) planted under different tree density levels of Chinese fir plantations were analyzed. The results demonstrated that growth rate and leaf functional traits could be used as a guide for selection of appropriate species for under-planting in thinned pure monoculture plantations to establish conifer-broadleaved mixed forests. This is because a low to intermediate tree density lowers the degree of shading and thus favors the growth of all under-planted species; particularly *T. odorum* seedlings. Specific leaf area and leaf N content predicts well root collar diameter growth of the species. Based on its better growth performance and high specific leaf area, *T. odorum* seedlings are suitable for planting under low tree density of Chinese fir plantation to established mixed-species forests followed by *M. macclurei* seedlings while *P. bournei* and *S. superba* are more appropriate for planting under dense stands as they tolerate shading. As a whole, our findings provide valuable insights about the role of leaf functional traits in evaluating species suitable for establishment of mixed species forest. Thus, forest managers should consider growth rate when selecting species for under-planting to establish mix-species forest and specific leaf area could be used as a guide to evaluate suitable species.

Author Contributions: Conceptualization, X.M. and M.L.; Formal analysis, R.X. and L.W.; Funding acquisition, P.W. and M.L.; Investigation, R.X., L.W., J.Z. (Jian Zhang), J.Z. (Jing Zhou), S.C.; Methodology, R.X., L.W., X.M. and M.L.; Supervision, M.L.; Validation, M.T.; Visualization, R.X. and L.W.; Writing—original draft, R.X.; Writing—review & editing, M.T. All authors have read and agreed to the published version of the manuscript.

Funding: This work was financially supported by the National Key Research and Development Program of China (2021YFD2201304).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data set used in this study can be made available from the authors upon reasonable request.

Acknowledgments: We thank staff members of the institute of forest and environment, college of Forestry, Fujian Agriculture and Forestry University for valuable discussion and assistance in field-work.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Felton, A.; Nilsson, U.; Sonesson, J.; Felton, A.M.; Roberge, J.M.; Ranius, T.; Ahlström, M.; Bergh, J.; Björkman, C.; Boberg, J.; et al. Replacing monocultures with mixed-species stands: Ecosystem service implications of two production forest alternatives in Sweden. *Ambio* **2016**, *45* (Suppl. S2), S124–S139. [[CrossRef](#)] [[PubMed](#)]
2. Li, C.M.; Du, J.S.; Zhang, H.R. Research of the Influence of Thinning on Forest Growth and Its Model. *For. Res.* **2003**, *16*, 636–641.
3. Xu, J.L.; Mao, Y.M.; Zheng, C.Z.; Fan, R.D.; Zhou, S.S.; Chen, Y.H.; Cheng, X.G.; Yu, M.K. Effect of Thinning on Growth and Timber Outturn in *Cunninghamia lanceolata* Plantation. *For. Res.* **2014**, *27*, 99–107.
4. Huang, Z.Q.; Wan, X.H.; He, Z.M.; Yu, Z.P.; Wang, M.H.; Hu, Z.H.; Yang, Y.S. Soil microbial biomass, community composition and soil nitrogen cycling in relation to tree species in subtropical China. *Soil Biol. Biochem.* **2013**, *62*, 68–75. [[CrossRef](#)]
5. Liu, L.; Duan, Z.H.; Wang, S.L.; Hu, J.C.; Hu, Z.G.; Zhang, Q.R.; Wang, S.J. Effect of *Cunninghamia lanceolata* Plantations at different development stage on soil microbial community structure. *Chin. J. Ecol.* **2009**, *12*, 2417–2423.
6. Zhao, Z.; Xue, D.Z.; Su, Y.Q.; Zhang, F.L. Study on the Benefits of Mixed Forest of *Pinus tabulaeformis* and *Platycladus orientalis* and the Relationship between Species. *J. Northwest For. Univ.* **1994**, *1*, 12–17.
7. Forrester, D.I.; Tang, X. Analyzing the spatial and temporal dynamics of species interactions in mixed species forests and the effects of stand density using the 3-PG model. *Ecol. Model.* **2016**, *319*, 233–254. [[CrossRef](#)]
8. Manson, D.G.; Hanan, J.; Hunt, M.; Bristow, M.; Erskine, P.D.; Lamb, D.; Schmidt, S. Modelling predicts positive and negative interactions between three Australian tropical tree species in monoculture and binary mixture. *For. Ecol. Manag.* **2006**, *233*, 315–323. [[CrossRef](#)]
9. Liu, X.J.; Ma, K.P. Plant Functional Traits-Concepts, Applications and Future Directions. *Sci. Sin. Vitae* **2015**, *45*, 325–339. [[CrossRef](#)]

10. Lei, L.J.; Kong, D.L.; Li, X.M.; Zhou, Z.X.; Li, G.Y. Plant functional traits, functional diversity, and ecosystem functioning: Current knowledge and perspectives. *Biodivers. Sci.* **2016**, *24*, 922–931. [CrossRef]
11. Garnier, E.; Navas, M.-L. A trait-based approach to comparative functional plant ecology: Concepts, methods and applications for agroecology, A review. *Agron. Sustain. Dev.* **2011**, *32*, 365–399. [CrossRef]
12. Laughlin, D.C.; Leppert, J.J.; Moore, M.M.; Sieg, C.H. A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Funct. Ecol.* **2010**, *24*, 493–501. [CrossRef]
13. Wright, I.J.; Reich, P.B.; Westoby, M.; Ackerly, D.D.; Baruch, Z.; Bongers, F.; Cavender-Bares, J.; Chapin, T.; Cornelissen, J.H.; Diemer, M.; et al. The worldwide leaf economics spectrum. *Nature* **2004**, *428*, 821–827. [CrossRef] [PubMed]
14. Wright, S.J.; Kitajima, K.; Kraft, N.J.; Reich, P.B.; Wright, I.J.; Bunker, D.E.; Condit, R.; Dalling, J.W.; Davies, S.J.; Díaz, S.; et al. Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* **2006**, *91*, 3664–3674. [CrossRef] [PubMed]
15. Martinez-Garza, C.; Bongers, F.; Poorter, L. Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? *For. Ecol. Manag.* **2013**, *303*, 35–45. [CrossRef]
16. Poorter, L.; Bongers, F. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **2006**, *87*, 1733–1743. [CrossRef]
17. Bhusal, N.; Bhusal, S.J.; Yoon, T.-M. Comparisons of physiological and anatomical characteristics between two cultivars in bi-leader apple trees (*Malus × domestica* Borkh.). *Sci. Hortic.* **2018**, *231*, 73–81. [CrossRef]
18. Vemmos, S.N.; Petri, E.; Stournaras, V. Seasonal changes in photosynthetic activity and carbohydrate content in leaves and fruit of three fig cultivars (*Ficus carica* L.). *Sci. Hortic.* **2013**, *160*, 198–207. [CrossRef]
19. Zeng, S.Q.; Gan, J.J.; Xiao, H.H.; Liu, F.L.; Xiao, B.S.; Peng, Q.L.; Wu, J. Changes in soil properties in regenerating *Schima superba* secondary forests. *Acta Ecol. Sin.* **2014**, *34*, 4242–4250.
20. Franklin, K.A. Shade avoidance. *New Phytol.* **2008**, *179*, 930–944. [CrossRef]
21. Sun, J.W.; Luo, L.Y.; Li, S.Y.; Wang, G.J.; He, G.X.; Wen, S.Z. Response of *Phoebe bournei* leaf functional traits and phenotypic plasticity to its mixture with the Chinese fir. *Acta Ecol. Sin.* **2021**, *41*, 2855–2866.
22. Li, X.; Liao, L.N.; Yang, H.P.; Huang, Y.Z.; He, A.J.; Ye, S.M. Spatial Pattern of Artificial Mixed Forest of *Cunninghamia lanceolata* and *Michelia macclurei*. *J. Southwest For. Univ.* **2020**, *40*, 1–9.
23. Rosati, A.; Day, K.R.; Dejong, T.M. Distribution of leaf mass per unit area and leaf nitrogen concentration determine partitioning of leaf nitrogen within tree canopies. *Tree Physiol.* **2000**, *20*, 271–276. [CrossRef] [PubMed]
24. Meng, J.; Luo, Y.H.; Yu, Y.; Liu, Z.Y.; Lin, J.Y. Latitudinal Variation of Branchlet Biomass Allocation and Functional Traits of Endangered Species *Tsoongiodendron Odorum* and Its Influencing Factors. *Guihaia*. 2021. Available online: <https://kns.cnki.net/kcms/detail/45.1134.Q.20210413.1553.002.html> (accessed on 11 June 2021).
25. Sun, S.Y.; Lu, S.X.; Lu, Y.M.; Xu, E.L.; Wu, D.M.; Liu, C.H.; Jiang, Z.K.; Guo, J.F. Effects of interplanting broad-leaved trees in Chinese fir forest on soil ecological enzyme activities and their stoichiometric ratios. *For. Res.* **2021**, *34*, 106–113.
26. Evans, J.R.; Poorter, H. Photosynthetic acclimation of plants to growth irradiance: The relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant Cell Environ.* **2001**, *24*, 755–767. [CrossRef]
27. Ma, X.Q. A review for research of productivity plantations after successive decline in Chinese fir plantings. *J. Fujian Coll. For.* **2001**, *21*, 380–384.
28. Zheng, Y. The Spatial and Temporal Variation of Plant Leaf and Fine Root Traits in the Yanhe River Catchment. Master's Thesis, Northwest Agriculture and Forestry University, Xianyang, China, 2014.
29. Zhang, S.M. Study on Leaf Economic Spectrum of Several Typical Deciduous Oaks (*Quercus*) in China. Master's Thesis, Shandong University, Jinan, China, 2020.
30. Farooq, T.H.; Wu, W.; Tigabu, M.; Ma, X.; He, Z.; Rashid, M.H.U.; Gilani, M.M.; Wu, P. Growth, Biomass Production and Root Development of Chinese fir in Relation to Initial Planting Density. *Forests* **2019**, *10*, 236. [CrossRef]
31. Alcorn, P.J.; Pyttel, P.; Bauhus, J.; Smith, R.G.B.; Thomas, D.; James, R.; Nicotra, A. Effects of initial planting density on branch development in 4-year-old plantation grown *Eucalyptus pilularis* and *Eucalyptus cloeziana* trees. *For. Ecol. Manag.* **2007**, *252*, 41–51. [CrossRef]
32. Wang, C. Effect of planting density on knot attributes and branch occlusion of *Betula alnoides* under natural pruning in southern China. *Forests* **2015**, *6*, 1343–1361. [CrossRef]
33. Nielsen, W.A.; Gerrand, A.M. Growth and branching habit of *Eucalyptus nitens* at different spacing and the effect on final crop selection. *For. Ecol. Manag.* **1999**, *123*, 217–229. [CrossRef]
34. Tun, T.N.; Guo, J.; Fang, S.; Tian, Y. Planting spacing affects canopy structure, biomass production and stem roundness in poplar plantations. *Scand. J. For. Res.* **2018**, *33*, 464–474. [CrossRef]
35. Dong, T.; Zhang, Y.; Zhang, Y.; Zhang, S. Continuous planting under a high density enhances the competition for nutrients among young *Cunninghamia lanceolata* saplings. *Ann. For. Sci.* **2015**, *73*, 331–339. [CrossRef]
36. Kearney, D. Characterization of Branching Patterns, Changes Caused by Variations in Initial Stocking and Implications for Silviculture, for *E. grandis* and *E. pilularis* Plantations in the North Coast Region of NSW. Master's Thesis, The Australian National University, Canberra, Australia, 1999; p. 89.
37. Aref, I.; El-Juhany, L.; Nasroon, T. Pattern of above-ground biomass production and allocation in *Leucaena leucocephala* trees when planted at different spacing. *Saudi J. Biol. Sci.* **1999**, *6*, 27–34.

38. Xue, L.; Pan, L.; Zhang, R.; Xu, P.B. Density effects on the growth of self-thinning *Eucalyptus urophylla* stands. *Trees* **2011**, *25*, 1021–1031. [[CrossRef](#)]
39. Liu, Q.; Huang, Z.; Wang, Z.; Chen, Y.; Wen, Z.; Liu, B.; Tigabu, M. Responses of leaf morphology, NSCs contents and C:N:P stoichiometry of *Cunninghamia lanceolata* and *Schima superba* to shading. *BMC Plant Biol.* **2020**, *20*, 354. [[CrossRef](#)]
40. Cardoso, D.J.; Lacerda, A.E.B.; Rosot, M.A.D.; Garrastazú, M.C.; Lima, R.T. Influence of spacing regimes on the development of loblolly pine (*Pinus taeda* L.) in Southern Brazil. *For. Ecol. Manag.* **2013**, *310*, 761–769. [[CrossRef](#)]
41. Giordano, P.A.; Hibbs, D.E. Morphological response to competition in red alder: The role of water. *Funct. Ecol.* **1993**, *7*, 462–468. [[CrossRef](#)]
42. Pienaar, L.V.; Shiver, B.D. Early results from an old-field loblolly pine spacing study in the Georgia Piedmont with competition control. *South J. Appl. For.* **1993**, *17*, 193–196. [[CrossRef](#)]
43. Yang, J.; Ci, X.; Lu, M.; Zhang, G.; Cao, M.; Li, J.; Lin, L. Functional traits of tree species with phylogenetic signal covary with environmental niches in two large forest dynamic plots. *J. Plant Ecol.* **2014**, *7*, 115–125. [[CrossRef](#)]
44. Zeng, Z.X.; Wang, K.L.; Liu, X.L.; Zeng, F.P.; Song, T.; Peng, W.X.; Zhang, H.; Du, H. Stoichiometric characteristics of live fresh leaves and leaf litter from typical plant communities in a karst region of northwestern Guangxi, China. *Acta Ecol. Sin.* **2016**, *36*, 1907–1914.
45. Pérez-Harguindeguy, N.; Díaz, S.; Garnier, E.; Lavorel, S.; Poorter, H.; Jaureguiberry, P.; Bret-Harte, M.S.; Cornwell, W.K.; Craine, J.M.; Gurvich, D.E.; et al. New handbook for standardised measurement of plant functional traits worldwide. *Aust. J. Bot.* **2016**, *64*, 715–716. [[CrossRef](#)]
46. Hessen, D.O.; Agren, G.I.; Anderson, T.R.; Elser, J.J.; de Ruiter, P.C. Carbon sequestration in ecosystems: The role of stoichiometry. *Ecology* **2004**, *85*, 1179–1192. [[CrossRef](#)]
47. Elser, J.J.; Bracken, M.E.S.; Cleland, E.E.; Gruner, D.S.; Harpole, W.S.; Hillebrand, H.; Ngai, J.T.; Seabloom, E.W.; Shurin, J.B.; Smith, J.E. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* **2007**, *10*, 1135–1142. [[CrossRef](#)] [[PubMed](#)]
48. Peterson, A.G. Reconciling the apparent difference between mass- and area-based expressions of the photosynthesis-nitrogen relationship. *Oecologia* **1999**, *118*, 144–150. [[CrossRef](#)]
49. LeBauer, D.S.; Treseder, K.K. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* **2008**, *89*, 371–379. [[CrossRef](#)]
50. Agren, G.I. Stoichiometry and nutrition of plant growth in natural communities. *Annu. Rev. Ecol. Evol. Syst.* **2008**, *39*, 153–170. [[CrossRef](#)]
51. Zeng, D.H.; Chen, G.S. Ecological stoichiometry: A Science to explore the complexity of living Systems. *Acta Phytoecol. Sin.* **2005**, *29*, 1007–1019.
52. Zhang, M.; Zhu, J.J.; Li, M.C.; Zhang, G.Q.; Yan, Q.L. Different light acclimation strategies of two coexisting tree species seedlings in a temperate secondary forest along five natural light levels. *For. Ecol. Manag.* **2013**, *306*, 234–242. [[CrossRef](#)]
53. Chen, Z.C.; Liu, X.J.; Liu, C.; Wan, X.C. Responses of growth, photosynthesis and nonstructural carbohydrate of *Quercus aliena* var. *acuteserrata* seedlings to shading and simulated sunfleck. *Chin. J. Ecol.* **2017**, *36*, 935–943.
54. Kono, Y.; Ishida, A.; Saiki, S.-T.; Yoshimura, K.; Dannoura, M.; Yazaki, K.; Kimura, F.; Yoshimura, J.; Aikawa, S. Initial hydraulic failure followed by late-stage carbon starvation leads to drought-induced death in the tree *Trema orientalis*. *Commun. Biol.* **2019**, *2*, 8. [[CrossRef](#)]
55. Huang, J.J.; Wang, X.H. Leaf Nutrient and Structural Characteristics of 32 Evergreen Broad-leaved Species. *J. East China Norm. Univ.* **2003**, *1*, 92–97.
56. Paine, T.C.E.; Amisshah, L.; Auge, H.; Baraloto, C.; Baruffol, M.; Bourland, N.; Bruelheide, H.; Dainou, K.; de Gouvenain, R.C.; Doucet, J.L.; et al. Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. *J. Ecol.* **2015**, *103*, 978–989. [[CrossRef](#)]
57. Bhusal, N.; Lee, M.; Lee, H.; Adhikari, A.; Han, A.R.; Han, A.; Kim, H.S. Evaluation of morphological, physiological, and biochemical traits for assessing drought resistance in eleven tree species. *Sci. Total Environ.* **2021**, *779*, 146466. [[CrossRef](#)] [[PubMed](#)]