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Variations in Leaf Functional Traits and Photosynthetic Parameters of *Cunninghamia lanceolata* Provenances

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Abstract: Studying the variation and correlation of traits among provenances is of great significance for the selection of excellent provenances and the interpretation of the acclimation mechanisms of different provenances in the context of climate change. The photosynthetic characteristic parameters and leaf functional traits of 18 *Cunninghamia lanceolata* provenances in a common garden were measured. Redundancy analysis combined with Pearson analysis was used to analyze the relationship among leaf photosynthetic characteristics, functional traits, and geo-climatic conditions. The results showed the following: (1) Significant differences in functional traits and photosynthetic parameters among provenances were observed, and the gsw and LDMC have the greatest variation as photosynthetic indicators and functional traits, respectively, because of the acclimation ability. (2) Leaf functional traits can better reflect the variation of photosynthetic characteristic parameters. The correlation between most photosynthetic characteristic parameters and functional traits reached a significant level ($p < 0.05$), and the leaf dry weight (LDW) and specific leaf area (SLA) are key trait factors that determine photosynthetic characteristic parameters. (3) Precipitation appeared to be a key factor that influences intraspecific leaf traits' variability compared to temperature. This study can explain how provenances acclimate to the environment and which provenances are more suitable for planting in the study area under the context of climate change from a mechanistic perspective.

Keywords: common garden; acclimation mechanism; geo-climatic conditions

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1. Introduction

Photosynthesis is one of the most basic physiological processes in plants, which converts light energy into chemical energy for plant growth and development [1]. Photosynthesis is not only affected by external environmental factors such as light, temperature, water, and CO_2 concentration but also by leaf characteristics [2]. Additionally, plant leaves not only undertake the important mission of photosynthesis but also play an important role in hydraulic transmission. The soil–plant atmosphere continuum relies on them for material and energy exchange [3,4]. As quantitative indicators of plant functional traits, leaf functional traits can respond to environmental changes and are relatively easy to measure. So, the functional traits of plant leaves and their relationship with ecosystem function are popular research topics for ecological scholars [5]. Leaf functional traits such as specific leaf area, leaf shape index, chlorophyll content, and leaf chemometric characteristics all reflect the acclimation changes made by plants to environmental conditions during long-term evolution and serve as a bridge between plants and the environment [6]. Leaf traits

determine the physiological attributes and functions of plants such as photosynthetic rate (Pn), transpiration rate (Tr), and nutrient intake [7]. Generally, plants acclimate to adverse conditions and reduce water loss by increasing the dry matter content of their leaves to increase construction costs, which reflects a resource conservation strategy [8], whereas higher specific leaf area, leaf N and P content, and other characteristics represent plant resource acquisition strategies [9]. Further, studies have shown that many trait relationships weaken within the species, with only leaf economic spectrum-related relationships maintaining good at inter-species and intra-species levels. Consequently, the relationship between certain traits within species may undergo significant changes in the context of future climate change, as well as ecological processes associated with these traits. As a result, it is necessary to pay attention to the intra-specific trait relationships and the important mechanisms that underline them [10]. It is particularly important to determine leaf functional traits in common gardens in order to analyze different provenances' response mechanisms to environmental conditions, their cascade relationships, and how different provenances' productivity is formed and optimized.

Using a large-scale study of functional traits and the environment is conducive to revealing the adaptive mechanism of species to the environment [11], while reducing the research scale to a common garden may reduce the impact of environmental factors, which may have a great deal of significance in explaining environmental filtering effects [12]. A common garden is a comparative afforestation experiment conducted by planting provenances from different geographical sites under the same conditions. A common garden provides a convenient environment for comparing the acclimation ability of different provenances to the local environment [13]. It is possible to determine stable and productive provenances and provide much-needed reliable information for forest management in the context of climate change by studying the regularity and spatial pattern of forest geographic variation and their interrelationships with the ecological environment [14]. Moreover, studying the relationship between leaf traits and photosynthetic characteristics in common gardens can reveal the acclimation mechanism and survival strategy of provenances in the context of changing climate [15].

Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook) is an important tree species for afforestation in southern China, due to its good wood properties and easy processing capabilities [16]. There are 16 provinces where this species is spread, including the southern edge of the warm temperate zone, the northern edge of the tropical zone, and the southern edge of the subtropical zone [17]. According to the ninth forest resource inventory report [18], the area of Chinese fir plantations is 9.902 million hm^2, accounting for 17.33% of the total forest area, and the storage volume is 755.4501 million cubic meters, accounting for 22.30% of the total, ranking first in the area and storage of artificial arbor forests in China. The selection of tree species provenance plays an important role in tree genetic improvement and the foundation of tree breeding [19]. In 1976, China established a national Chinese fir geographical provenance experiment collaboration group to carry out Chinese fir provenance experiments due to the limited application of improved Chinese fir varieties and the low productivity during afforestation [20]. This project aims to fully utilize the geographical variation of Chinese fir provenances to select and utilize Chinese fir provenances for afforestation, and to improve the productivity of Chinese fir plantations in the short term. On this basis, a large number of studies had been conducted by the experimental collaboration group on selecting provenance, determining cold resistance, drought resistance, disease resistance, wood properties, and growth drought period, as well as estimating genetic parameters and dividing provenance regions of Chinese fir. The results demonstrate the variation in acclimation between widely dispersed Chinese fir and different geographical environments and climates. In early provenance experiments, attention was usually paid to the differences in fast-growing traits after introduction and cultivation, while ignoring the evaluation from a physiological and ecological perspective [21]. Due to its wide distribution and high economic value, there has been more and more research on functional traits and the productivity of Chinese fir, providing references

for the mechanism by which productivity is formed in future climate change scenarios and a scientific basis for selecting excellent provenances [22].

In this study, we investigated leaf-level functional traits and gas exchange characteristics of Chinese fir from 18 provenances grown in a common garden at Dagangshan, Jiangxi, China. The common garden approach enabled us to disentangle the latitudinal effects and environmental effects on the trait variability. Specifically, we hypothesized that (1) there are significant differences in functional traits and gas exchange characteristics at the provenance level; (2) the functional traits are important factors affecting inter-species photosynthetic characteristics; and (3) despite the fact that the provenance acclimates to the hydrothermal conditions of the study area, environmental factors from the origin of the provenance can still be a significant factor in explaining the differences in traits among provenances. This study provides insights into potential mechanisms influencing traits' variation among provenances. It is also helpful to understand the reasons for the formation of the current geographical distribution pattern of Chinese fir. The results provide a "stethoscope" function for the precise cultivation of reserve forests in southern China.

2. Materials and Methods

2.1. Study Site

The study site is located at Dagangshan Forest Ecosystem National Field Scientific Observation Research Station in Fenyi County, Jiangxi Province, 27°30′~27°50′ N and 114°30′~114°35′ E (Figure 1). It belongs to the branch of Wugong Mountain in the northern section of the Luoxiao Mountains. The soil type is red and yellow soil [23]. The Dagangshan region is located in the central subtropical region, with a subtropical monsoon humid climate. The average annual temperature is 16.8 °C, and the average annual rainfall is 1590.1 mm. Rainfall is concentrated from April to June. In 1981, the Chinese Academy of Forestry conducted a geographical provenance experiment of Chinese fir at Dagangshan, which established a common garden containing 183 Chinese fir provenances. In this study, we selected 18 provenances (Table 1) growing in the common garden in Dagangshan for 41 years under the same climatic conditions with consistent slope orientation, soil, and altitude conditions, located in adjacent groups during the provenance experiment's design (Figure 1) [20], for the determination of photosynthetic characteristic parameters and leaf functional traits (Table 1). The geographic locations of the studied provenance were recorded with hand-held GPS. The meteorological data came from the Meteorological Data Center of the National Meteorological Administration of China (http://data.cma.cn/, 1 July 2023), and the meteorological data of the sampling points are the average values from 1980 to 2010.

Table 1. Geo-climatic information of provenance origin used in this study.

	Provenance	Longitude	Latitude	Mean Annual Temperature (°C)	Mean Annual Precipitation (mm)	Growing Season Mean Temperature (°C)	Growing Season Precipitation (mm)
1	Zhaoping, Guangxi	110°50′ E	24°11′ N	20.1	1992.6	23.96	1613.8
2	Mengshan, Guangxi	110°32′ E	24°14′ N	19.9	1741.2	23.84	1443.9
3	Changting, Fujian	116°22′ E	25°41′ N	18.5	1712.1	22.51	1279.9
4	Yangxin, Hubei	115°13′ E	29°15′ N	17.5	1454.3	22.53	1138.7
5	Wufeng, Hubei	110°20′ E	25°24′ N	14.9	1307.4	19.15	1161.2
6	Rongshuisirong, Guangxi	117°30′ E	30°13′ N	19.1	1992.6	23.38	1612.6
7	Shitai, Anhui	119°22′ E	29°14′ N	16.1	1797.6	20.88	1388.1
8	Yongchang, Zhejiang	119°50′ E	24°11′ N	16.1	1423.1	21.1	1099.7
9	Yunhe, Zhejiang	119°35′ E	28°07′ N	17.9	1631.5	22.32	1259.5
10	Longquan, Zhejiang	119°08′ E	28°05′ N	18	1649.2	22.29	1249.7
11	Shanghang, Fujian	116°25′ E	25°04′ N	20.3	1666.9	24	1304.5
12	Fenyi, Jiangxi	114°43′ E	27°49′ N	17.9	1640.9	22.64	1216.7
13	Lingchuan, Guangxi	109°13′ E	25°13′ N	20.98	1431.1	25.03	1184.7
14	Yongfu, Guangxi	110°00′ E	24°60′ N	19.1	1963.9	23.29	1590.1

Table 1. *Cont.*

	Provenance	Longitude	Latitude	Mean Annual Temperature (°C)	Mean Annual Precipitation (mm)	Growing Season Mean Temperature (°C)	Growing Season Precipitation (mm)
15	Dehua, Fujian	117°48′ E	26°24′ N	18.8	1739.7	23.5	1239.8
16	Sanming, Fujian	117°39′ E	26°46′ N	19.6	1665.2	23.39	1238
17	Shaxian, Fujian	118°15′ E	25°30′ N	18.3	1823.3	21.75	1488.6
18	Hongya, Sichuan	103°22′ E	29°55′ N	16.8	1385	20.68	1282.8

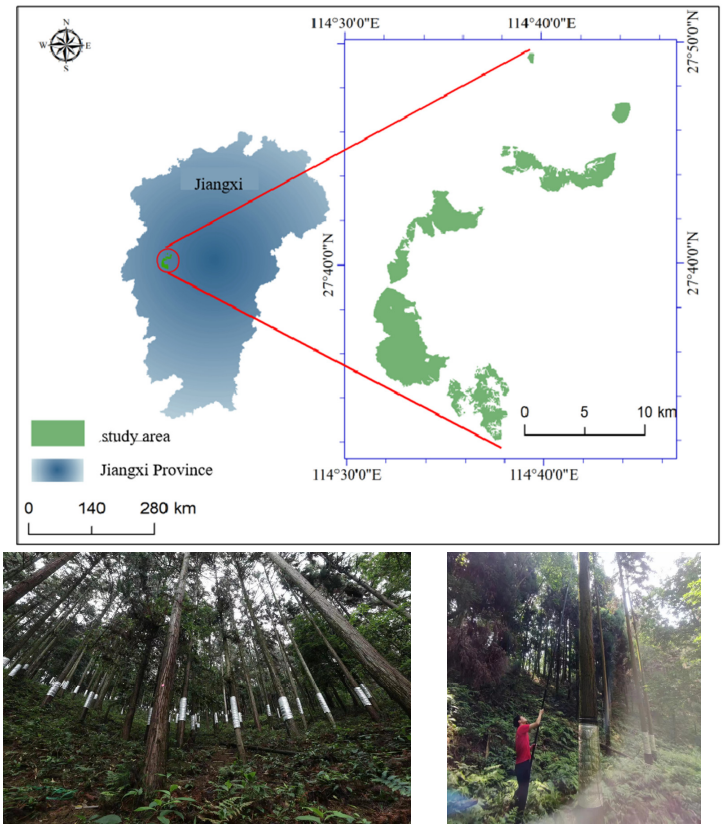


Figure 1. Study area and collecting samples in the common garden.

2.2. Measurements of Leaf Functional Traits

In August 2021, we selected three trees from each provenance and 20 healthy leaves on the second node of each tree for the measurement of leaf functional traits. The leaf functional traits were as follows: leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), and soil and plant analyzer development (SPAD). LA was determined by scanning the leaves with an Epson 110 scanner and analyzing the images using area measurement software from Image J. Leaf fresh weight (LFW) was weighed. SPAD value was measured with SPAD-502 by cleaning and drying the fresh Chinese fir leaves and selecting 5 points evenly in the middle of each living leaf (avoiding the midrib) to read the relative chlorophyll content. The average value is used as the SPAD value of the leaf. Then all leaf samples were oven-dried at 80 °C for 72 h to constant mass and weighed for their dry weight (LDW). Then, leaf samples were ground to a fine powder. The leaf 13C/12C were analyzed using a vario MICRO cube elemental analyzer (Elementar Ltd., Hanau, Germany) coupled with an isotope ratio mass spectrometer (IsoPrime, Manchester, UK). The calculation of leaf carbon isotope composition (δ13C) leaf was calculated as follows:

$$\delta 13C = \left[\left(R_{sample} / R_{standard} \right) - 1 \right] \times 1000, \quad (1)$$

The SLA was calculated for each leaf as the ratio of leaf area to leaf dry mass. LDMC was computed as the ratio of leaf dry mass to leaf saturated fresh mass [24]:

$$SLA = LA/LDW, \quad (2)$$

$$LDMC = LDW/LFW \quad (3)$$

2.3. Measurements of Gas Exchange Characteristics

The gas exchange parameters of leaves of different provenances were measured with a LI-6800 portable photosynthetic analyzer (LI-COR Company, Lincoln, NE, USA). The gas exchange parameters include the maximum net photosynthetic rate (Pn), stomatal conductance (gsw), intercellular CO_2 concentration (Ci), environmental CO_2 concentration (Ca), and transpiration rate (Tr). The specific measurement method for the maximum net photosynthetic rate is as follows: In August 2021, on sunny days from 09:00 a.m. to 11:00 a.m., three adjacent healthy living leaves with a central sunny direction were collected from three Chinese fir trees in each provenance, nine leaves in total for each provenance; the branches were quickly inserted into the water. The LI-6800 portable photosynthetic (LI-COR company in the United States) was used to measure the maximum net photosynthetic rate of Chinese fir leaves. The parameter settings of the photosynthetic apparatus refer to the study conducted by Xiao et al. [25] on the photosynthesis of Chinese fir forests in this region. The light intensity set for the instant photosynthetic measurement was 2000 μmol·(m^2·s^{-1}), and the leaf chamber temperature was set to 25 °C. We calculated the stomatal limit values (Ls) and water use efficiency (WUE) using the following formula:

$$WUE = Pn/Tr, \quad (4)$$

$$Ls = 1 - Ci/Ca, \quad (5)$$

2.4. Data Analysis

An analysis of variance (ANOVA) was conducted as part of the analysis to examine the intraspecific variations in leaf functional traits among provenances at the $p < 0.05$ level. To conduct multiple comparisons among provenances when significant differences were observed, the Duncan post hoc test was used. Additionally, we calculated the coefficient of variation (CV), which is defined as the ratio of standard deviation to the average value across provenances. All data were expressed as the mean ± standard error (SE). Redundancy analysis (RDA) was used to examine the relationships among leaf functional traits, gas exchange characteristics, and geo-climatic conditions of the provenance origin. Lastly, Pearson correlation analysis was used to examine the relationship between traits. SPSS 24.0 software was used for ANOVA and correlation analyses, while Canoco (Version 5) was used for RDA.

3. Results

3.1. Variations in Leaf Functional Traits

The leaf traits and photosynthetic characteristics of various provenances are shown in Figure 2. There were significant variations in photosynthetic and leaf functional traits that were observed among provenances ($p < 0.01$). The CV of leaf functional traits ranges from 7.88% to 2.03%, with the greatest variation occurring in LDMC value and the smallest variation occurring in leaf fresh weight. In terms of variation between photosynthetic characteristics, the CV ranges from 8.38% to 27.37%, with Tr exhibiting the lowest degree of variation and gsw exhibiting the highest degree of variation. From the perspective of leaf traits, the LA of various provenances ranges from 0.84 cm^2 to 1.15 cm^2, with the maximum value appearing in Longquan and the minimum value appearing in Hongya, with an average value of 1.01 cm^2; SPAD value ranges from 19.4 to 35.3, with the maximum

value appearing in Wufeng and the minimum value appearing in Dehua, with an average value of 26.1; SLA ranged from 95.51 $cm^2 \cdot g^{-1}$ to 179.12 $cm^2 \cdot g^{-1}$, with an average value of 135.46 $cm^2 \cdot g^{-1}$. The maximum value appeared in provenance 11, and the minimum value appeared in provenance 17; the LDWC ranged from 17.70% to 36.62%, with an average value of 25.90%. The maximum value appeared in Shaxian and the minimum value appeared in Shanghang. From the perspective of photosynthetic characteristic parameters, the Pn of various provenances is between 2.06 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$~4.76 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$; the maximum value appears in Shaxian, and the minimum value appears in Hongya, with an average value of 3.03 $\mu molCO_2 \cdot m^{-2} \cdot s^{-1}$. Tr ranges from 1.63 $mmolH_2O \cdot m^{-2} \cdot s^{-1}$ to 2.19 $mmolH_2O \cdot m^{-2} \cdot s^{-1}$, with the maximum value appearing in Sanming, the minimum value appearing in Longquan, and an average value of 1.85 $mmolH_2O \cdot m^{-2} \cdot s^{-1}$. WUE ranges between 1.16 $\mu molCO_2 \cdot mmolH_2O$ and 2.28 $\mu molCO_2 \cdot mmolH_2O$; the maximum value appears in Shaxian, and the minimum value appears in Hongya, with an average value of 1.63 $\mu molCO_2 \cdot mmolH_2O$. Ls ranges from 0.27 to 0.60, with the maximum value appearing in Shaxian, the minimum value appearing in Yunhe, and an average value of 0.41.

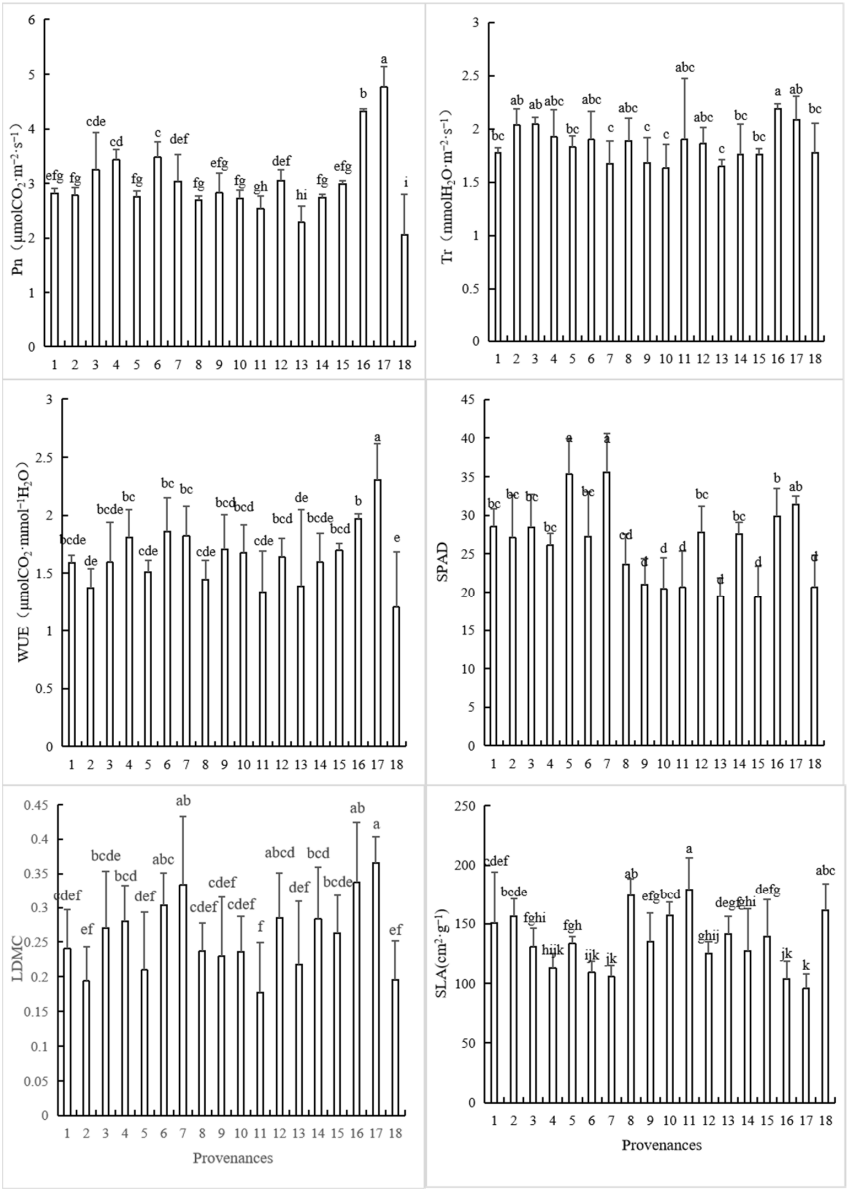


Figure 2. Leaf traits and photosynthetic characteristics of Chinese fir provenance. Different letters indicate significant differences among provenances.

3.2. Correlations among Leaf Functional Traits

The correlation analysis between leaf functional traits and photosynthetic parameters is shown in Table 2. From the perspective of photosynthetic characteristics, Tr is significantly positively correlated with Gs ($p < 0.05$); Pn is significantly positively correlated with Tr, WUE, and Gs ($p < 0.01$); WUE is significantly positively correlated with gsw ($p < 0.01$); and other parameter correlations have not reached a significant level. From the perspective of leaf functional traits, the SPAD value showed a significant positive correlation ($p < 0.05$) with LDW and LDMC and a significant negative correlation ($p < 0.01$) with SLA. LDW was significantly negatively correlated ($p < 0.01$) with SLA and significantly positively correlated ($p < 0.01$) with LDMC, and a significant negative correlation ($p < 0.01$) was shown between SLA and LDMC.

From the perspective of the correlation between leaf photosynthetic characteristic parameters and leaf functional traits, Pn is significantly positively correlated with SPAD at the $p < 0.05$ level, significantly positively correlated with LDW, and significantly positively correlated with LDMC at the $p < 0.01$ level, and it is significantly negatively correlated with SLA ($p < 0.01$). A significant positive correlation exists between WUE and LDW and LDMC ($p < 0.01$), and a significant negative correlation exists between WUE and SLA ($p < 0.01$). Moreover, gsw is significantly positively correlated with SPAD at the $p < 0.05$ level, and it is significantly positively correlated with LDW, has a significant positive correlation with LDMC at the $p < 0.01$ level, and has a significant negative correlation with SLA ($p < 0.01$).

Table 2. Correlation coefficients of functional traits of Chinese fir provenances.

	δ13C	**Tr**	**Pn**	**WUE**	**Ci**	**Ls**	**gsw**	**SPAD**	**LFW**	**LDW**	**LA**	**SLA**	**LDMC**
δ13C	1												
Tr	−0.084	1											
Pn	−0.006	0.689 **	1										
WUE	0.014	0.35	0.918 **	1									
Ci	0.1	−0.015	−0.011	0.027	1								
Ls	−0.098	0.015	0.013	−0.026	−0.999 **	1							
gsw	−0.168	0.508 *	0.873 **	0.871 **	0.124	−0.123	1						
SPAD	−0.171	0.367	0.493 *	0.456	0.227	−0.229	0.484 *	1					
LFW	−0.27	0.119	−0.046	−0.101	0.069	−0.071	0.047	−0.082	1				
LDW	−0.109	0.417	0.903 **	0.949 **	0.034	−0.033	0.860 **	0.545 *	−0.091	1			
LA	0.127	0.084	0.156	0.184	0.04	−0.039	0.308	−0.167	0.365	0.187	1		
SLA	0.186	−0.302	−0.767 **	−0.828 **	−0.081	0.080	−0.706 **	−0.614 **	0.258	−0.876 **	0.279	1	
LDMC	−0.004	0.346	0.836 **	0.893 **	0.029	−0.027	0.777 **	0.547 *	−0.429	0.936 **	0.043	−0.881 **	1

* represent the significant relation at the 0.05 level, ** represent the significant relation at the 0.01 level. Tr: transpiration rate, Pn: photosynthetic rate, gsw: stomatal conductance, Ci: intercellular. CO_2 concentration, WUE: water use efficiency, Ls: stomatal limit values, LA: leaf area, SLA: specific leaf area, LDMC: leaf dry matter content, LFW: leaf fresh weight, LDW: leaf dry weight, δ13C: leaf carbon isotope composition.

Redundancy Analysis was performed to examine the relationship between gas exchange characteristics of provenances and leaf functional traits. The RDA analysis results show that the feature values on the first and second sorting axes are 0.4495 and 0.1103 (Figure 3), respectively, with a cumulative interpretation rate of 55.98% and an overall interpretation rate of 58.80%. The first two ranking axes explained 76.43% and 18.76% of the total variation of leaf photosynthetic characteristic parameters, with a cumulative explanatory capacity of 95.19%. Therefore, it can be concluded that the correlation between leaf functional traits and photosynthetic characteristic parameters can be well explained, and the first ranking axis plays a decisive role. Leaf dry weight and specific leaf area are key trait factors that determine photosynthetic characteristic parameters, with contribution rates of 74.6% and 12.8%, respectively.

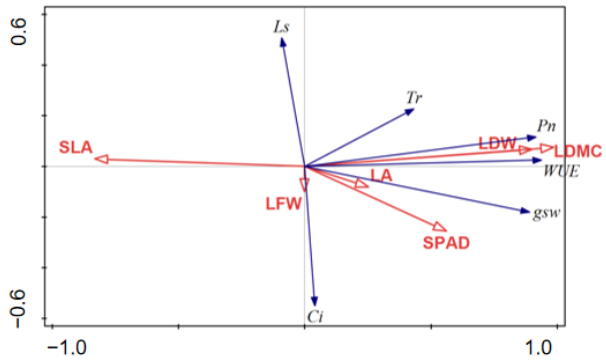


Figure 3. RDA analysis of leaf traits and photosynthetic characteristics of Chinese fir provenance. Tr: transpiration rate, Pn: photosynthetic rate, gsw: stomatal conductance, Ci: intercellular CO_2 concentration, WUE: water use efficiency, Ls: stomatal limit values, LA: leaf area, SLA: specific leaf area, LDMC: leaf dry matter content, LFW: leaf fresh weight, LDW: leaf dry weight, δ13C: leaf carbon isotope composition.

3.3. Relationship between Geo-Climatic Conditions of Provenances and Leaf Functional Traits of Provenances

Redundancy Analysis was performed to examine the relationship between geo-climatic conditions of provenances and leaf functional traits (Figure 4). The results showed that longitude, growing season precipitation, and the mean annual precipitation were positively correlated with the δ13C, WUE, Ci, LDMC, LDW, Pn, Tr, LA, gsw while they were negatively correlated with SLA. Latitude was negatively correlated with δ13C, WUE, Ci, LDMC. Growing season temperature and mean annual temperature were positively correlated with LFW, SLA, and Ls, but they were negatively correlated with δ13C, WUE, Ci, LDMC. The RDA analysis results show that the feature values on the first and second sorting axes are 0.2238 and 0.0663, respectively. The explanatory variables account for 39.4%. The first two ranking axes explained 56.82% and 16.83% of the total variation of leaf functional traits, with a cumulative explanatory capacity of 73.65%.

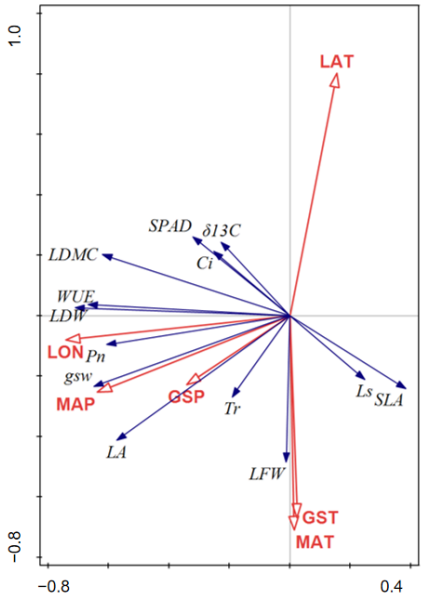


Figure 4. RDA analysis of leaf traits and geo-climatic conditions. Tr: transpiration rate, Pn: photosynthetic rate, gsw: stomatal conductance, Ci: intercellular CO_2 concentration, WUE: water use efficiency, Ls: stomatal limit values, LA: leaf area, SLA: specific leaf area, LDMC: leaf dry matter content, LFW: leaf fresh weight, LDW: leaf dry weight, δ13C: leaf carbon isotope composition, Lon: longitude, LAT: latitude, MAT: mean annual temperature, MAP: mean annual precipitation, GST: growing season mean temperature, GSP: growing season precipitation.

4. Discussion

There is evidence that the same species undergoes geographical variation, leading to geographical provenances. The degree of variation in their functional traits determines their range of adaptation to the environment [26]. Halik et al. found that the CV of plant traits generally does not exceed 30% [27]. In this study, the variation in leaf traits of Chinese fir from different provenances ranged from 7.88% to 2.03%, and the CV of different photosynthetic characteristic parameters ranged from 8.38% to 27.37%, which is consistent with previous findings. The degree of variation in LDMC values is the highest among leaf traits, while the degree of variation in gsw is the highest among photosynthetic traits, indicating that there is a large selection space among individuals from different sources of Chinese fir. The LFW has the lowest CV among leaf functional traits, while the Tr variation among photosynthetic functional traits is the smallest, indicating a smaller space for future trait selection. Survival strategies are closely related to SLA as an important indicator of plant utilization and preservation environmental resources [28]. The larger CV of SLA in this study indicates significant differences in resource acquisition and utilization abilities among different provenances. The SPAD value represents the relative content of chlorophyll in leaves and is widely used in crops such as soybeans, wheat, and corn [29]. It characterizes the ability of plants to capture light energy, with a CV of 19.20%, indicating significant differences in light energy capture ability among different provenances. This can also be confirmed by the variation characteristics of Pn (CV = 21.02%).

There is an inverse relationship between functional traits and acclimation to environmental changes during the plant evolution [30]. The results of this study are in agreement with those of others that find SLA negatively correlated with Tr and Pn [31]. In many studies, it has also been confirmed that SLA is significantly negatively correlated with LDMC [32]. As SLA increases, leaf tissue density decreases and leaf water content increases, leading to a decrease in LDMC. The trade-off and covariation between the two are to respond to and adapt to habitat changes [33]. Moreover, LDMC is positively correlated with WUE and Pn. WUE, as an important indicator of carbon water coupling, characterizes the carbon assimilation ability of plants under unit water consumption [34]. Therefore, species with high WUE may accumulate more dry matter and have higher LDMC. It has been found that SPAD and Pn are significantly positively correlated, suggesting that provenances with a high SPAD are able to capture more light energy, indicating that provenances with high chlorophyll content have stronger photosynthetic capacity [35]. Some studies have shown a significant positive correlation between the $\delta 13C$ and WUE calculated through gas exchange method [36], while others have shown a weak correlation [37]. Therefore, studying the variability and coupling relationship between instantaneous and long-term water use efficiency of Chinese fir provenances is of great significance for in-depth research on the water and carbon processes of different provenances and for more accurate screening of Chinese fir provenances. We found that there was a loose relationship between $\delta 13C$ and WUE. It is possible that instantaneous water use efficiency may differ from long-term water use efficiency due to the influence of environmental factors such as photosynthetic active radiation, stomatal conductance, intercellular CO_2 concentration, air CO_2 concentration, air temperature, leaf temperature, and air humidity [38].

Among geo-climatic factors of the provenance origin, longitude and precipitation had influence on the functional traits of Chinese fir. There was a correlation between the provenance origin's climate conditions and its traits, but it was not statistically significant. Chinese fir provenance from Dehua, Fujian, had the smallest SLA, the largest LDMC, the highest WUE, and the highest Pn. This provenance is characterized by good precipitation conditions. Similarly, Chinese fir provenance from Lingchuan, Guangxi, which is also characterized by high mean annual precipitation conditions, had high WUE and Pn. These good water conditions favor a high photosynthetic rate that, in turn, resulted in large leaf mass investment [39]. The SLA was high for Chinese fir from Yongchang, Zhejiang; Shanghang, Fujian; and Hongya, Sichuan, where the temperature is relatively high and the precipitation is relatively few in these region. Thus, high SLA offers an acclimation to

capture more light resources to optimize photosynthetic rate under these conditions [40]. Previous studies have shown similar results in which precipitation affects functional traits and productivity [21]. In our study, we found that the variability of intraspecific traits is influenced by the mean annual precipitation. In other studies, temperature has been found to be a key factor governing intraspecific variability in water consumption traits [41].

From the perspective of leaf traits and photosynthetic characteristics, it was found that different provenances such as Rongshuisirong, Guangxi; Shaxian, Fujian; and Dehua, Fujian showed higher water and light utilization efficiency. Nine provenances had a better ability to acquire resources than the local provenance (Fenyi, Jiangxi). Based on the research of Wu et al. [17], it can be seen that the provenances mentioned above exhibit faster growth in long-term selection. This study has also been proven from the perspective of leaf traits and photosynthetic characteristics. To a certain extent, we provide another approach for screening high-quality provenances in this study. As a result of the process of acclimation to environment, different provenances exhibit different characteristic responses. Future research will examine the relationship between long-term water use efficiency and the instantaneous water use efficiency for various Chinese fir provenances, and the growth characteristics of various provenances will be used to screen the excellent provenances.

5. Conclusions

Based on the measurement of functional traits and photosynthetic parameters among *Cunninghamia lanceolata* provenances, we clarified the significant physiological characteristics variation among provenances. Our findings show the relationship among leaf functional traits, environmental factors of provenances' origin, and photosynthetic parameters in a common garden. The differences in photosynthetic and leaf functional traits among different provenances reached a highly significant level ($p < 0.01$). Leaf functional traits can better reflect the variation of photosynthetic characteristic parameters, and the relationship between most traits and WUE reaches a highly significant level. Leaf dry weight (LDW) and specific leaf area (SLA) are key trait factors that determine photosynthetic characteristic parameters. Mean annual precipitation appeared to be a key factor that influences intraspecific leaf traits variability compared to mean annual temperature. These findings provide new insights into understanding the intrinsic mechanism of differences in provenances growth and acclimation to changing climate in a common garden.

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