

Article

Effects of Slope Position on Morphological, Anatomical, and Chemical Traits of *Cunninghamia lanceolata* (Lamb.) Hook. Fine Roots

Linxin Li, Jing Liang, Yunlong Tian, Ming Li, Xiangqing Ma, Aiqin Liu * and Pengfei Wu * 

Chinese Fir Engineering Technology Research Center of State Forestry Administration, College of Forestry, Fujian Agriculture and Forestry University, Fuzhou 350002, China; lilinlinzy@163.com (L.L.);

fjyangjoung@126.com (J.L.); fafutyl@126.com (Y.T.); limingly@126.com (M.L.); lxxmxq@126.com (X.M.)

* Correspondence: fjlq@126.com (A.L.); fjwupengfei@126.com (P.W.); Tel.: +86-18060546607 (A.L.); +86-13635281431 (P.W.)

Abstract: Fine root traits and their relationships reflect the ecological trade-off strategies of plants in resource investment and are important for understanding the life strategies and growth of plants in response to changes in the environment. We used 16-year-old Chinese fir (*Cunninghamia lanceolata* Lamb. Hook.) plantations with different slope positions as the research object to explore the morphological, anatomical, and chemical properties of fine roots and their relationships. With increasing root order levels, the morphological, anatomical, and chemical traits of the fine roots of Chinese fir at different slope positions showed similar change trends; however, at the same order level, the differences were large. Under the upper slope site conditions, the average diameter of the second- and third-order roots and the thickness of the third-order root cortex were the highest. However, specific surface area, vascular bundle diameter, and the ratio of third-order roots were higher under the middle-slope site conditions. Under the lower slope site conditions, the specific surface area and specific root length of first-order roots and the root ratio of second-order roots were the highest. The biomasses of the first- and third-order roots on the middle and lower slopes were higher than those on the upper slope. The contents of N and P in fine roots of grades 1–3 Chinese fir showed the order of lower slope > middle slope > upper slope; however, the changes in C/N and C/P ratios showed the opposite trend, indicating differences in the morphological, anatomical, and chemical properties as well as resource acquisition strategies of fine roots of grades 1–3 Chinese fir under different slope positions. There were negative correlations between fine root diameter, N and P contents, and specific root length, indicating an acquisition and conservative resource trade-off relationships between fine root morphological, anatomical, and chemical traits. There were also differences in the relationships between the morphological, anatomical, and chemical traits of Chinese fir fine roots at different slope positions, indicating that the relationships between these traits were affected by slope position change. Chinese fir varieties with root-foraging characteristics ranging from resource conservation to resource acquisition can be selected for planting to improve the productivity of *C. lanceolata* plantations.

Keywords: *Cunninghamia lanceolata*; soil water and nutrients; root order; functional properties; trade-off relationship



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1. Introduction

Fine roots growing at the root end, with a diameter of less than 2 mm, are the most sensitive underground parts of plants to environmental changes and play an important role in plant nutrient absorption and soil carbon and nutrient cycling [1]. Fine root growth, death, and decomposition directly affect the functioning of terrestrial ecosystems, especially the search for and absorption of limited water and fertilizer resources in the soil, such as nitrogen, phosphorus, and water [2]. Owing to the plasticity and changing characteristics of roots, in the process of long-term adaptation to changing environments, they interact

with the surrounding soil, showing significant ecological effects on the rhizosphere [3]. At the evolutionary time scale, fine roots continue to evolve a wide range of underground strategies to optimize the rhizosphere environment and obtain these limited resources while responding to their availability in a timely manner to better supply nutrients and water to the aboveground plant organs [4]. Fine roots may generate multidimensional root trait economic spaces that represent nutrient acquisition strategies for multi-trait combinations [5]. However, the soil environment in which roots grow is heterogeneous, with phosphorus restricting aboveground plant growth in terrestrial ecosystems [6]. The niche distribution of soil water and fertilizer resources in the vertical and horizontal directions determines the degree of fine root differentiation and may simultaneously drive the expression of fine root traits in multiple directions at the same time [7]. In particular, the roots growing in extremely phosphorus-deficient soils have a wider range of comprehensive root characteristics because fine roots need to rationalize the use of limited resources to balance multiple traits and avoid wasting resources [8]. In production, slope position has a direct impact on the spatial distribution and configuration of regional water and fertilizer resources, as well as light and heat conditions, and is a common topographic limiting factor for plant growth and development. Studies have shown that in the long-term evolution process, fine roots respond to the differences in the soil microenvironment caused by slope positions through the synergy of multiple traits, thereby supporting plant growth [9].

Chinese fir (*Cunninghamia lanceolata*) is a high-quality, fast-growing, evergreen coniferous tree that is mainly planted in southern China. The plantation area is 9.920 million hm^2 , with a volume of 755.4501 million m^3 , accounting for 7.56% of the world's plantation area [10,11]. Owing to the fast growth, wide planting area, and long-term continuous cropping of Chinese fir, the nutrient consumption of forest land is large, and the sustainable management of Chinese fir plantations is facing problems such as deterioration of soil quality and declining productivity. In addition, owing to the interference of human activities, the soil nutrient contents of Chinese fir plantations vary greatly in time and space, especially in the red soils of southern China, where phosphorus deficiency is serious; available phosphorus easily combines with Al^{3+} , Fe^{3+} , or Ca^{2+} ; and its mobility is poor [12]. The contents of ammonium nitrogen ($\text{NH}_4^{4+}\text{-N}$) and nitrate nitrogen ($\text{NO}_3^{3-}\text{-N}$), which are the main nitrogen elements that can be absorbed and utilized, are also very low in the soil. In addition, during a rotation period of nearly 25 years, a large amount of P is removed from the forestland with the harvesting of trees, resulting in a decrease in the available P content in the soil surface layer, which cannot maintain the long-term productivity of Chinese fir plantations [13,14]. To alleviate the sharp decline in soil quality in Chinese fir forests, a series of studies have been conducted to improve the long-term productivity of the plantations from the aspects of genetics, sites, and density control of Chinese fir [15,16]. In recent years, with deepening research on the structure and function of underground roots, it has become important to explore the long-term maintenance and improvement of the productivity of Chinese fir plantations from the perspective of the ability of roots to absorb resources. Therefore, studying fine root traits helps solve the problem of long-term productivity maintenance in Chinese fir plantations.

In a previous study of Chinese fir fine roots, it was found that harsh environmental conditions, such as drought and acidity, led to the growth of more root tips (first-order roots), and the root system changed to the acquisition foraging strategy. In fertile areas with more abundant rainfall and neutral soil, clumping mycorrhizal colonization rates are higher, and roots shift to conservative foraging strategies [17]. The plasticity of the fine roots plays an important role in this process. Specific root length, specific root area, and specific root tip density of Chinese fir fine roots in mature forests show a decreasing trend with increasing forest age, and the nutrient foraging ability decreases; however, physiological compensation occurs by increasing the nitrogen concentration of the fine roots [18]. By observing the cross-sectional microstructure of the fine roots of Chinese fir, it was found that the activity of the cambium was significantly increased in an environment with sufficient phosphorus, which promoted an increase in root diameter and biomass

and improved the quality of seedlings [19]. With increasing research on the relationship between global environmental change and root systems, fine roots are an important bridge connecting the external morphology, internal physiological activity, and functions of plants. Multi-trait functions of fine roots have been widely used to quantitatively study and predict the response and adaptability of plants to various environments [20]. Due to the influence of slope position, there are differences in the microbial communities in the soil in Chinese fir forestland, with varying metabolites secreted by fine roots that are related to defense/nutrient acquisition functions. Thus, fine roots of Chinese fir under different slope positions likely have their own life strategies for absorbing and utilizing nutrients [9]. However, for the fine roots of Chinese fir, although there is a certain degree of understanding of the functional structure of single traits, there is still a lack of understanding of multi-trait combinations and their relationships.

The purpose of this study was to determine whether the fine root traits of Chinese fir plantations change with different soil water and fertilizer resources. We explored how these traits worked together to help the roots adapt to different environments. We measured and analyzed the morphological, chemical, and anatomical traits of fine roots in Chinese fir plantations at different slope positions and their relationships. The results of this study are conducive to further understanding the ecological strategies of resource investment and income balance of Chinese fir through synergistic changes in fine roots and multiple traits and provide a scientific basis for improving the productivity and sustainable management of Chinese fir plantations. The main hypotheses were as follows: (1) The slope position leads to different degrees of soil water and fertilizer resources. Owing to changes in root plasticity, the fine roots of Chinese fir effectively absorb the limited resources in the soil. (2) Influenced by changes in water and fertilizer resources in the soil where Chinese fir roots grow at different slope positions, Chinese fir forms a relationship between resource acquisition efficiency and maintenance costs by adjusting the internal relationship of fine root traits.

2. Materials and Methods

2.1. Study Area and Materials

2.1.1. Overview of the Study Area

The study area is located in the Baisha State-owned Forest Farm in Shanghang, Fujian Province, China (25°01′–25°16′ N, 116°20′–116°39′ E), with an altitude of 200–700 m and a slope of 10–40°. The terrain is high in the north and low in the south. The soil is mainly sandy red soil developed from coarse-grained granite. The soil layer was more than 60 cm thick. The site grades of the forest land were mainly classes II and III. The frost-free period in this area is 301 days, the average annual temperature is 20.1 °C, and the annual rainfall is 1600 mm. The understory herb layer plants mainly include *Lophatherum gracile* Brongn., *Dicranopteris dichotoma* (Thunb.) Bernh., *Woodwardia japonica* (L. f.) Sm., and *Miscanthus floridulus* (Labill.) Warburg ex K. Schumann.

2.1.2. Materials

In July 2022, a 16-year-old Chinese fir plantation on a forest farm was selected as the research object. The slope direction of the farm is consistent. The elevation gradient is in the range of 711.04–750.41°. Three 20 m × 20 m standard plots were set up on the upper, middle, and lower slopes for a total of nine standard plots, and adjacent plots had a boundary distance of at least 20 m (Figure 1). The growth of Chinese fir in each standard plot was measured for each tree, and the DBH was measured. The tree height was measured using an ultrasonic rangefinder (Vertex IV, Haglof, Långsele, Sweden). The average DBH and tree height of the Chinese fir in each standard plot were calculated, and three average trees were selected for a total of 27 trees. At the same time, the ring knife method and forest soil analysis method were used to determine the soil moisture and nutrients [21]. The chemical properties of these forests are listed in Table 1. In the surface soil at 0–20 cm, the contents of nitrogen, phosphorus, potassium, and available potassium in the soil increased gradually with decreasing slope position, and the nutrients were

gradually enriched. The physical properties of these forests are listed in Table 2. In the 0–20 cm surface soil, the water content increased with decreasing the slope position.

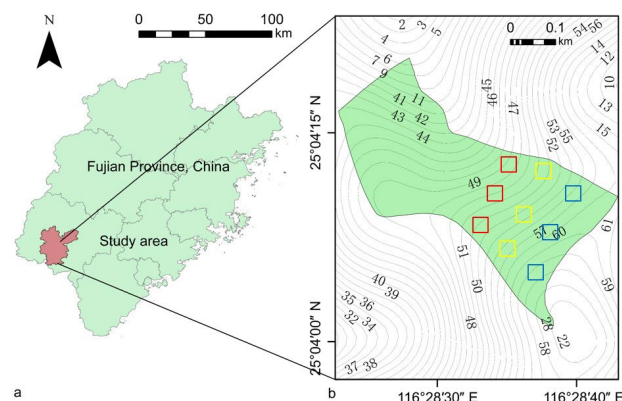


Figure 1. Geographical position of the study area. Red squares: upper slope; yellow squares: middle slope; blue squares: lower slope; (a) Fujian Province, China; (b) study area (Numbers are absolute elevations).

Table 1. Soil chemical properties at different slope positions within the 0–20 cm depth.

Slope	Carbon Content /g·kg ^{−1}	Nitrogen Content/g·kg ^{−1}	Phosphorus Content/g·kg ^{−1}	Potassium Content/g·kg ^{−1}	Calcium Content/g·kg ^{−1}	Magnesium Content/g·kg ^{−1}	Available Phosphorus Content/mg·kg ^{−1}	Available Potassium Content/mg·kg ^{−1}
Upper	32.40 ± 2.34 a	1.94 ± 0.33 c	0.21 ± 0.05 c	27.05 ± 0.91 c	0.95 ± 0.12 a	2.50 ± 1.17 a	2.56 ± 0.45 b	8.83 ± 0.68 c
Middle	27.78 ± 1.35 b	2.42 ± 0.18 a	0.22 ± 0.02 ab	30.60 ± 1.20 b	0.90 ± 0.46 a	1.30 ± 0.49 b	3.61 ± 0.94 a	11.23 ± 0.20 b
Lower	24.75 ± 1.27 c	2.20 ± 0.26 b	0.23 ± 0.01 a	32.32 ± 1.46 a	0.57 ± 0.03 b	2.25 ± 0.70 a	2.15 ± 0.44 c	12.34 ± 0.36 a

Note: The same lowercase letter indicates that the difference between different slope positions was not significant ($p > 0.05$).

Table 2. Soil physical properties at different slope positions within the 0–20 cm depth.

Slope	pH	Soil Bulk Density/g·cm ^{−3}	Soil Moisture Content/%	Capillary Moisture Capacity/%	Capillary Porosity/%	Noncapillary Porosity/%
Upper	3.81 ± 0.06 b	1.06 ± 0.08 a	20.95 ± 3.58 a	284.71 ± 48.85 a	14.42 ± 1.22 b	7.44 ± 0.94 b
Middle	4.14 ± 0.13 a	0.82 ± 0.03 b	23.26 ± 2.60 a	265.75 ± 18.39 b	18.33 ± 1.09 a	6.48 ± 1.76 b
Lower	4.13 ± 0.10 a	1.09 ± 0.09 a	23.44 ± 3.45 a	251.30 ± 33.35 b	18.73 ± 1.94 a	11.19 ± 2.40 a

Note: The same lowercase letter indicates that the difference between different slope positions was not significant ($p > 0.05$).

2.2. Research Methods

2.2.1. Root Sample Collection

At the base of the selected average trunk, the fine roots with complete root structure and diameter ≤ 2 mm were excavated according to the four directions of east, west, south, and north. The rhizosphere soil on the roots was gently shaken off, and dead roots and other impurities were removed and stored in a foam box at a low temperature. A total of 108 complete Chinese fir root samples were collected and immediately transported to the laboratory for testing.

2.2.2. Determination of Morphological Traits of Fine Roots of Chinese Fir of Different Ranks

The complete root samples were classified according to the root order method [22]. The roots with the tips at the front ends were defined as the first-order roots, the mother root of the first-order root was the second-order root, and the mother root of the second-order root was the third-order root. After grading, fine root samples of different orders were scanned using a digital scanner (STD 1600 Epson, Los Alamitos, CA, USA) combined with the root analysis system software WinRHIZO (Version4.0B, Rengent Instruments, Québec City, QC, Canada) to measure the mean diameter, length, surface area, volume, and other morphological indicators. After determination, the samples were placed in an oven at 105

°C for 30 min and dried to a constant weight at 80 °C for biomass determination. The tissue density, specific surface area, and specific root length of the fine roots of different orders of Chinese fir were calculated using the following formulas:

$$\text{Tissue density} = \text{root dry mass} / \text{root volume};$$

$$\text{Specific root length} = \text{root length} / \text{root dry matter weight};$$

$$\text{Specific surface area} = \text{root surface area} / \text{root dry matter mass}.$$

2.2.3. Determination of Anatomical Properties of Fine Roots of Chinese Fir of Different Ranks

Fine root samples of grades 1–3 were used as experimental materials and cut into small segments (each with a length of 0.5 cm); at least three segments were taken for each sequence-level sample. Microwave paraffin sectioning was performed to slice the samples of different thicknesses using a semithin sectioning machine (Leica RM2265, Wetzlar, Germany). Three transverse sections of the fine root samples were prepared in different orders from each plot. On average, 20–30 transverse sections of the fine roots were distributed in each section. Nine complete samples were randomly selected, photographed, and observed under a Nikon electron microscope (ECLIPSE 200, Tokyo, Japan). ScopeImage software (version 9.0) was used to analyze and measure the anatomical structural parameters, such as vascular bundle diameter, cortical thickness, stele area, root transverse section diameter, and root transverse section area of the fine roots at all levels. Based on the measured anatomical structural parameters, the ratio of stele to root diameter and the cortex ratios of fine roots in different orders of Chinese fir were calculated using the following formulas:

$$\text{Ratio of stele to root diameter} = \text{vascular bundle diameter} / \text{root cross-sectional diameter};$$

$$\text{Cortical ratio} = (\text{cortical area} / \text{entire root cross-cutting area}) \times 100.$$

The cortical area represents the difference between the transverse area of the entire root and the middle column.

2.2.4. Determination of Chemical Properties of Fine Roots of Chinese Fir of Different Ranks

Fine root samples of different orders were crushed and sieved (0.149 mm), and the carbon and nitrogen contents of the fine root tissues at all levels were determined using an automatic elemental analyzer (Vario Macro Cube, Elementar, Langenselbold, Germany). HNO₃-H₂O₂ microwave digestion (ETHOS UP, Shimadzu, Kyoto, Japan) and an inductively coupled plasma emission spectrometer (PE OPTIMA 8000, PerkinElmer, Shelton, CT, USA) were used to determine the phosphorus content. The C/N, C/P, and N/P ratios were calculated according to the carbon, nitrogen, and phosphorus contents in the fine root tissues at all levels.

2.3. Statistical Analysis

Excel 2019 was used for the data collection and table drawing. One-way ANOVA was used to compare the differences between the indicators, and the least significant difference (LSD) test was used to test the differences between the indicators ($p = 0.05$). The data analysis process was performed using the SPSS software (version 25.0), and normality and homogeneity of variance tests were performed before analysis ($p > 0.05$). Pearson's correlation analysis was performed using the Origin 2018 software. Regression analysis and the plotting of some graphs were performed using GraphPad Prism 9.5.1.733 software. The results are expressed as mean $\pm$ one standard error.

3. Results

3.1. Changes in Fine Root Morphological Traits of Chinese Fir at Different Slope Positions

Except for root tissue density, two factors, slope position and sequence level, had significant interactions with the determination indices of fine root morphological traits at

different sequence levels of Chinese fir ($p < 0.05$, Table 3). As a single factor, slope position had no significant effect on root tissue density ($p > 0.05$) but had a significant effect on the other indices ($p < 0.05$). The effect of order rank on all measured indices was significant.

Table 3. Two-way ANOVA results of slope position and root order on each measurement index of Chinese fir fine root morphological traits.

Influence Factor	Degree of Freedom/df	F Value				
		Root Average Diameter	Root Tissue Density	Specific Surface Area	Specific Root Length	Biomass
Slope	2	2.754 *	2.787	1.215 *	2.295 *	6.991 **
Root order	2	20.648 **	0.560 *	31.488 **	43.167 **	3.75 *
Slope $\times$ root order	4	1.003 *	2.216	0.777 *	0.484 *	0.760 *

* means significant difference ($p < 0.05$); ** means extremely significant difference ($p < 0.01$).

There were differences in the morphological traits of fine roots in the different orders of Chinese fir (Figure 2). With a decrease in slope position, the average diameter and tissue density of the 1–3 roots of Chinese fir increased gradually, the specific surface area and specific root length decreased gradually, and the biomass first decreased and then increased. The average diameter and specific root length of grades 1–3 roots were significantly different among the different slope positions ($p < 0.05$).

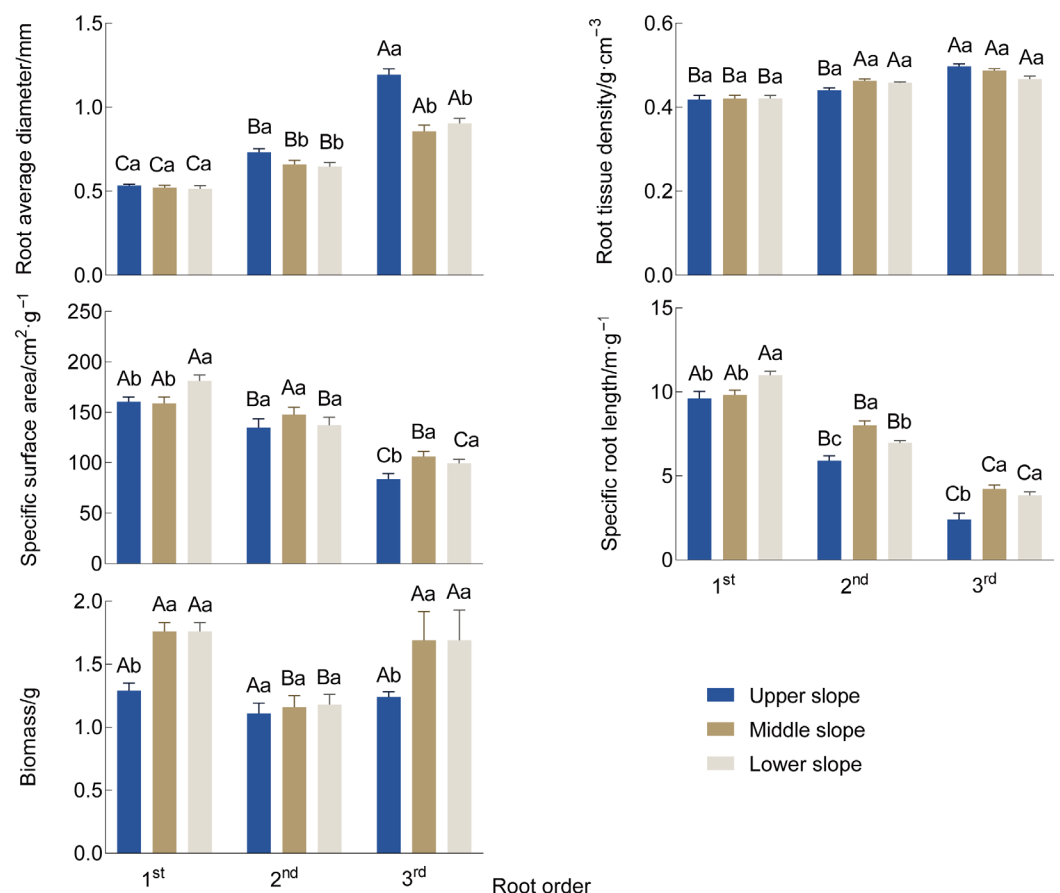


Figure 2. Comparison of fine root morphological traits of Chinese fir at different slope positions: 1st—first-order roots; 2nd—second-order roots; 3rd—third-order roots. Similar uppercase letters indicates that the difference between different root orders of the same slope position was not significant ($p > 0.05$). Likewise, similar lowercase letters indicate that the difference between different slope positions for the same root order was not significant ($p > 0.05$).

Similarly, the average diameter of the second-order roots (0.73 ± 0.02 mm) and third-order roots (1.19 ± 0.03 mm) at the upper slope were significantly larger than those at the middle and lower slopes. The specific surface area of the third-order roots at the middle slope was the largest, increasing by 26.72% and 6.89% compared with the upper and lower slopes, respectively, followed by the lower slopes. However, the specific surface area of the first-order roots was the largest, increasing by 12.88% and 14.10% compared with the upper and middle slopes, respectively. In addition, the specific root lengths of the second- and third-order roots at the middle slope were the largest, followed by those at the lower slope, and were the smallest at the upper slope. On the other hand, the specific root length of the first-order roots at the lower slope was the largest, with a value of 10.99 ± 0.23 m·g⁻¹. The biomasses of the first- and third-order roots at the middle and lower slopes were significantly greater than that at the upper slope, and the tissue density of the second-order roots was significantly greater than that of the upper slope.

3.2. Changes in Fine Root Anatomical Traits of Chinese Fir at Different Slope Positions

From the anatomical structure of fine roots of Chinese fir at different order levels, there were no significant differences in the basic organizational structure characteristics among the roots of ranks 1–3 (Figure 3). Root tissue structures such as vascular bundles, cortical parenchyma cells, and epidermis were evident. Cortical parenchyma cells occupied more root cross-sectional areas than the vascular bundles and other tissue structures.

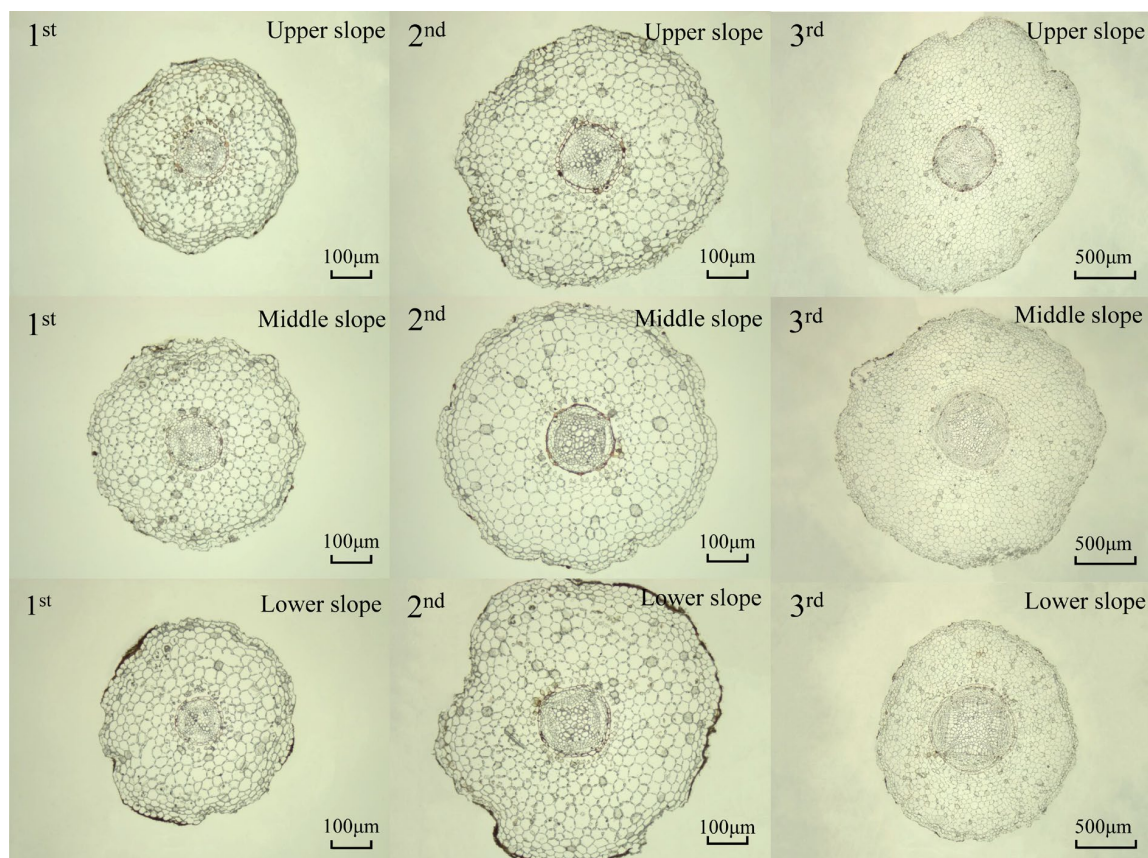


Figure 3. Anatomical structure characteristics of fine roots of Chinese fir from different slope positions: 1st—first-order roots; 2nd—second-order roots ($\times 10$); 3rd—third-order roots ($\times 4$).

The two factors of slope position and sequence level had a significant interaction with the fine root anatomical traits at different sequence levels of Chinese fir ($p < 0.05$; Table 4). From a single-factor point of view, the effects of slope position and order on the vascular bundle diameter, root ratio, cortical thickness, and cortical ratio were significant ($p < 0.05$).

Table 4. Two-way ANOVA results of slope position and root order for each measurement index of Chinese fir fine root anatomical traits.

Influence Factor	Degree of Freedom/df	Statistical Values/F			
		Vascular Bundle Diameter	Ratio of Stele to Root Diameter	Cortical Thickness	Cortical Ratio
Slope	2	23.527 **	11.493 **	4.080 *	17.795 **
Root order	2	1356.470 **	56.181 **	532.695 **	48.266 **
Slope × root order	4	26.018 **	10.123 **	5.243 **	13.642 **

* means significant difference ($p < 0.05$); ** means extremely significant difference ($p < 0.01$).

In terms of the anatomical traits of fine roots of different orders of Chinese fir, with a decrease in slope position, the vascular bundle diameter, the ratio of dimension to root, and the cortical thickness of grades 1–3 roots increased gradually (Figure 4). The vascular bundle diameter and cortical thickness of the grades 1–3 roots were significantly different among the different slope positions ($p < 0.05$). In the cortex ratio, only the cortex ratio of grades 1–2 roots at the middle slope was significantly greater than that of grade 3 roots. At the same sequence level, the cortical thickness of the third-order roots on the upper slope was significantly greater than those at the middle and lower slopes ($p < 0.05$). The vascular bundle diameter and vascular root ratio of the third-order roots at the middle slope were the largest, followed by those at the lower slope. The lowest vascular bundle diameter and vascular root ratio of the third-order roots were found at the upper slope. The diameter of the vascular bundles and the ratio of the vascular bundle diameter to the root diameter of the second-grade roots at the lower slope were the largest, followed by the upper slope. Those at the lower slope were the smallest. However, there were no significant differences in the diameter of the vascular bundles, the ratio of stele to root diameter, the thickness of the cortex, the ratio of the cortex to the roots of the first-order roots, the thickness of the cortex, or the ratio of the cortex to the roots of the second-order roots at different slope positions ($p < 0.05$).

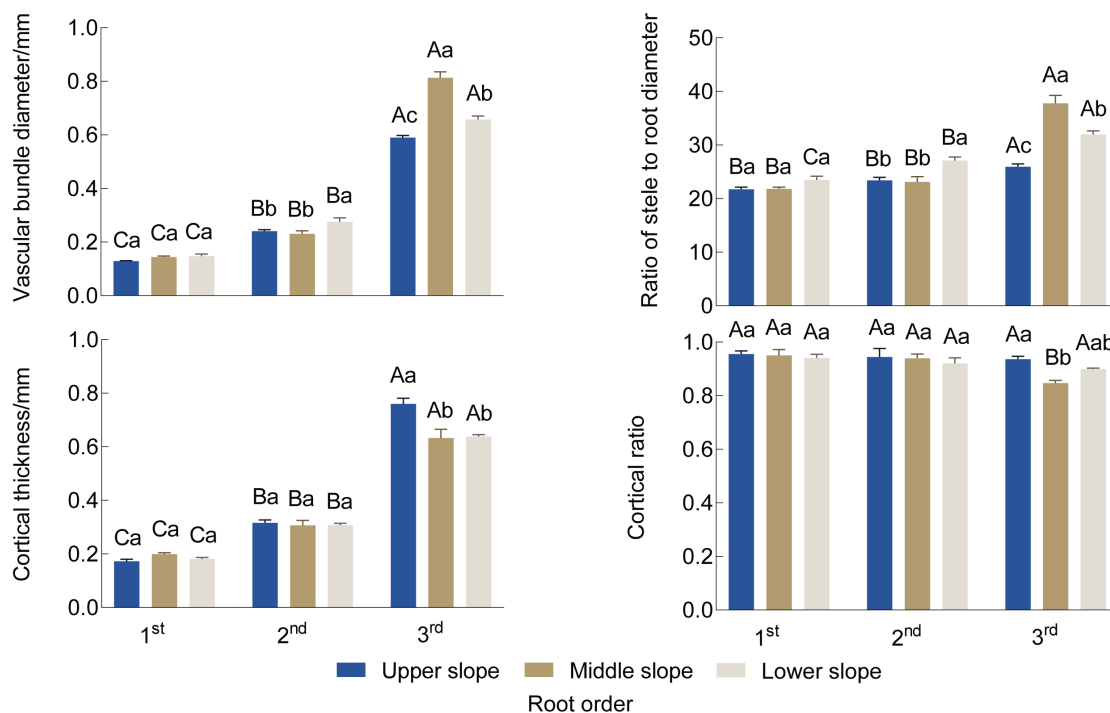


Figure 4. Comparison of fine root anatomical traits of Chinese fir at different slope positions. Similar uppercase letters indicates that the difference between different root orders of the same slope position was not significant ($p > 0.05$). Likewise, similar lowercase letters indicate that the difference between different slope positions for the same root order was not significant ($p > 0.05$).

3.3. Changes in Chemical Properties of Fine Roots of Chinese Fir from Different Slope Positions

There was no significant interaction between the two factors of slope position and root order level for the determination indices of fine root chemical properties at different order levels of Chinese fir ($p > 0.05$, Table 5). From a single-factor perspective, the effect of slope position on the fine root chemical traits was significant ($p < 0.05$).

Table 5. Two-way ANOVA results of slope position and root order on each measurement index of Chinese fir fine root chemical traits.

Influence Factor	Degree of Freedom/df	Statistical Values/F					
		Carbon Content	Nitrogen Content	Phosphorus Content	Carbon Nitrogen Ratio	Carbon Phosphorus Ratio	Nitrogen Phosphorus Ratio
Slope	2	0.785 *	18.032 **	0.898 *	21.346 **	9.056 **	0.162 *
Root order	2	2.855	8.824 **	6.437 **	8.73 **	2.188 *	0.78
Slope $\times$ root order	4	1.545	0.596	2.019	1.86	0.264	0.475

* means significant difference ($p < 0.05$); ** means extremely significant difference ($p < 0.01$).

With a decrease in slope position, the carbon content of the grades 1–3 roots first increased and then decreased, whereas nitrogen and phosphorus contents decreased gradually. In terms of the stoichiometric ratio, with a decrease in the slope position, the C/N and C/P ratios increased gradually, whereas the trend of the N/P ratio showed the opposite trend. At the same sequence level, the carbon content of the first-order roots at the lower slope was significantly higher than at the upper and middle slopes ($p < 0.05$). The nitrogen content of the first- to third-order roots was also significantly higher at the lower slope than at the upper and middle slopes. In addition, the phosphorus content of grades 1–3 roots at the middle and lower slopes was significantly higher than those at the upper slope, but the carbon–nitrogen and carbon–phosphorus ratios showed opposite trends. With respect to the nitrogen-to-phosphorus ratio, only second-order roots from the lower slope were significantly larger than those from the upper slope (Figure 5).

3.4. Relationship between Fine Root Morphological, Anatomical, and Chemical Properties of Chinese Fir

Typical indicators for the regression analysis were selected based on fine root morphological, anatomical, and chemical traits. From Figure 6, root diameter was negatively correlated with specific root length, nitrogen content, phosphorus content, and vascular bundle diameter, whereas cortical thickness was negatively correlated with nitrogen and phosphorus contents. Root diameter was positively correlated with vascular bundle diameter and cortex thickness, and specific root length was positively correlated with nitrogen and phosphorus contents. Except for the relationship between vascular bundle diameter and phosphorus content ($p < 0.05$), the relationship between cortical thickness and phosphorus content was not significant ($p > 0.05$), whereas the relationship between the other indicators was significant.

Correlations between the morphological, anatomical, and chemical traits of Chinese fir at different slope positions were analyzed (Figure 7). The results showed that the root diameter at different slope positions was negatively correlated with the specific root length ($p > 0.05$) and positively correlated with the diameter of the vascular bundles, root-to-root ratio, and cortical thickness. Specific surface area and specific root length were negatively correlated with other anatomical traits, except for the ratio of the cortex. Among the chemical traits, vascular bundle diameter and cortex thickness at different slope positions were positively correlated with nitrogen content. Only the specific surface area and specific root length of the upper slope were negatively correlated with nitrogen content, whereas the root diameter of the upper slope was positively correlated with nitrogen content.

Furthermore, the specific surface area and specific root length of the upper and lower slopes were positively correlated with the phosphorus content.

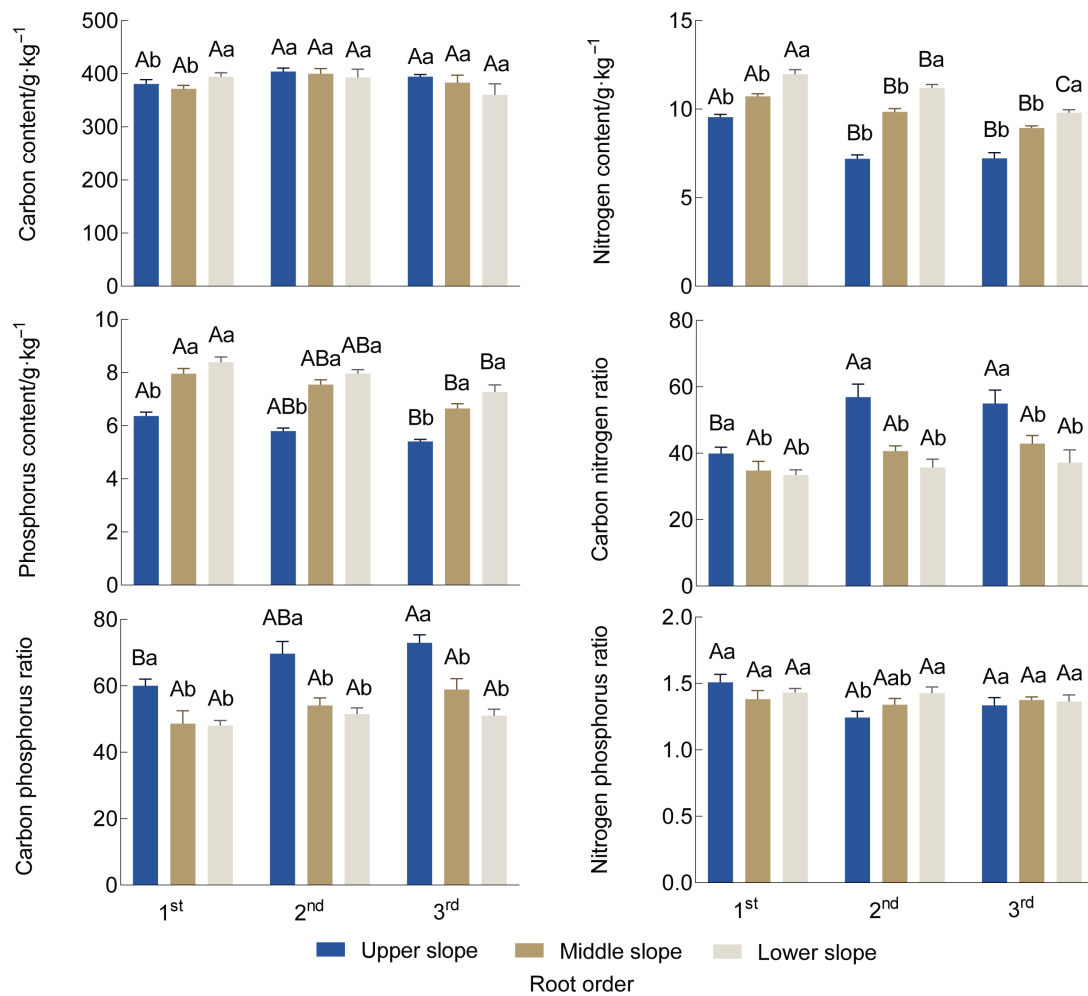


Figure 5. Comparison of chemical traits of fine roots of Chinese fir from different slope positions. Similar uppercase letters indicates that the difference between different root orders of the same slope position was not significant ($p > 0.05$). Likewise, similar lowercase letters indicate that the difference between different slope positions for the same root order was not significant ($p > 0.05$).

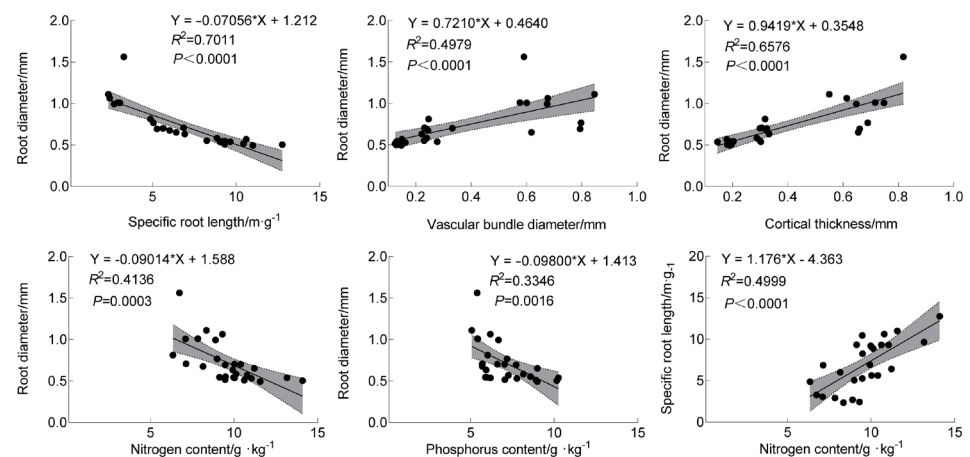


Figure 6. Cont.

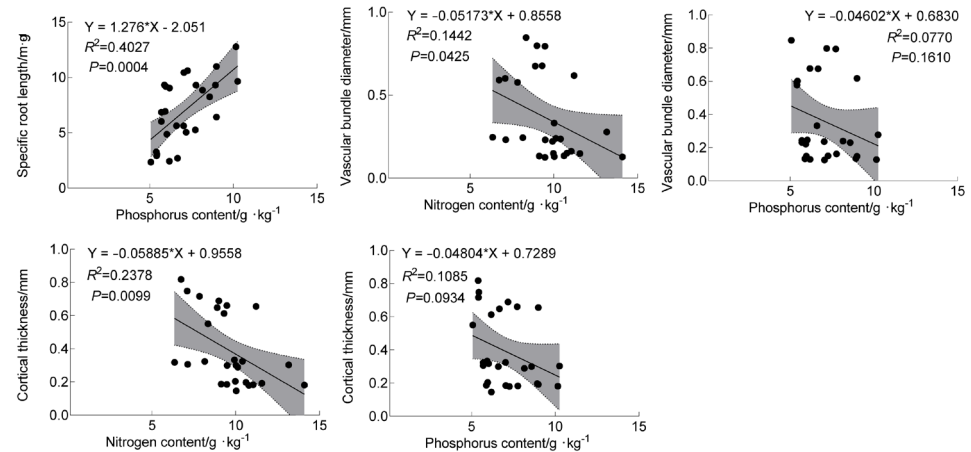


Figure 6. Regression analysis of morphological, anatomical, and chemical traits of fine roots of Chinese fir. * Indicates $\times$.

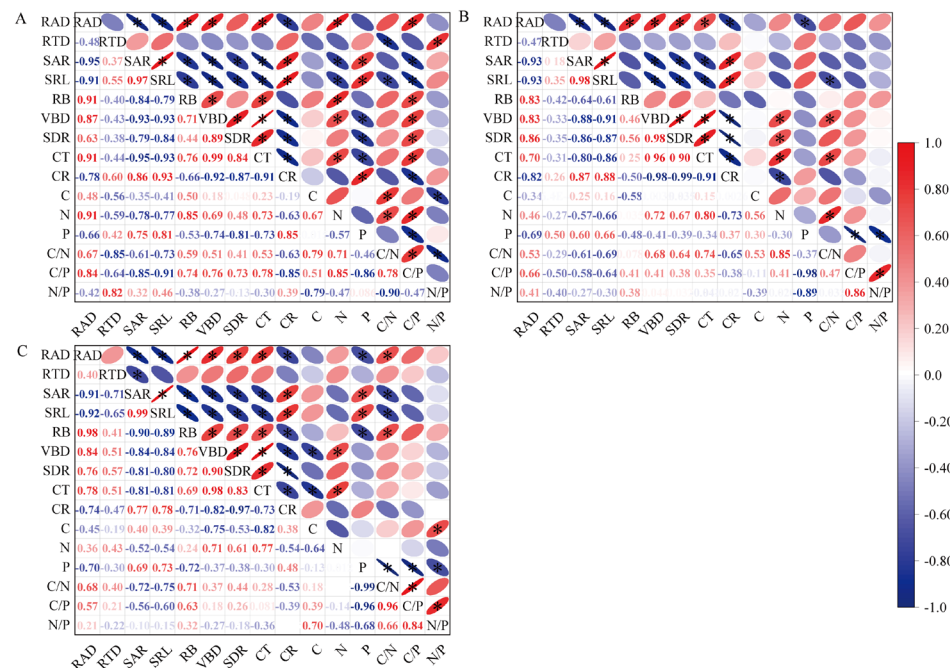


Figure 7. Correlation analysis between morphological, anatomical, and chemical traits of fine roots of Chinese fir from different slope positions. (A): upper slope; (B): middle slope; (C): lower slope. * indicates a significant correlation at $p < 0.05$ level (two tails). RAD: root average diameter; RTD: root tissue density; SAR: specific surface area; SRL: specific root length; RB: Root biomass; VBD: vascular bundle diameter; SDR: ratio of stele to root diameter; CT: cortical thickness; CR: cortical ratio; C: carbon content; N: nitrogen content; P: phosphorus content; C/N: carbon-to-nitrogen ratio; C/P: carbon-to-phosphorus ratio; N/P: nitrogen-to-phosphorus ratio.

4. Discussion

4.1. Regulatory Mechanism of Slope Location on Soil Resource Acquisition Strategies of Chinese Fir Fine Roots

Throughout the life cycle of fine roots, their morphological, anatomical, and physiological traits differ at the spatial and temporal scales and perform a variety of functions [23]. Fine root trait adjustment is an effective way for roots to optimize their structure and reduce life risks. It characterizes different strategies for obtaining soil resources but changes with the effectiveness of the soil resources [24]. In the present study, with an increase in the root order level, the trends in the morphological, anatomical, and chemical traits of the fine roots of Chinese fir at different slope positions were the same. Finer roots can penetrate the

soil matrix to explore soil resources more effectively and have a higher water acquisition capacity [25]. With an increase in the root order level, the diameter increases, indicating the transformation of the primary roots to the secondary roots, the gradual weakening of the absorption capacity, and a gradual increase in the transportation capacity, forming two different functional modules [8,26]. Thus, this change in the fine roots is related to a major functional shift from absorption to transport. However, at the same order level, the difference is large. In terms of fine root morphology, the average diameters of the second- and third-order roots were the largest at the upper slope. In a study of temperate trees and shrubs in North America, roots with smaller diameters per unit mass had a larger surface area and a stronger ability to obtain soil nutrients and water [27]. Therefore, compared with the middle and lower slopes, the main role of the grades 2–3 fine roots of Chinese fir at the upper slope was to transport nutrients. In addition, the specific surface area of third-order roots at the middle slope was the largest. In *Eucalyptus globulus* Labill. and *Acacia mearnsii* De Wild., the specific surface area reflects the nutrient use efficiency of fine roots in the soil [28]. Therefore, the fine roots of Chinese fir at the middle slope are more efficient at utilizing soil resources than those at the upper and lower slopes.

However, fine roots must regulate the transport and absorption of substances to balance resource acquisition and construction maintenance costs, which can be explored based on changes in specific root length and biomass [29]. In poor soils, investing more biomass to construct longer fine roots can improve the absorption efficiency of roots for resources per unit biomass investment; however, this has a negative impact on root longevity [30]. In this study, the specific root lengths of the second- and third-order roots at the middle slope were the largest, but the specific surface area and specific root lengths of the first-order roots at the lower slope were the largest. This further indicates that the fine roots of Chinese fir at the middle slope have a stronger ability to absorb and utilize resources, whereas the first-order roots of Chinese fir at the lower slope have a stronger ability to explore and absorb resources [17,28]. From the distribution pattern of biomass among fine roots, the biomass of the first- and third-order roots from the middle and lower slopes was greater than that of the roots from the upper slope. The greater the biological value, the higher the plant's expectation of return [31]. This shows that the resource limitation of Chinese fir growing at the upper slope is greater than that of Chinese fir growing at the middle and lower slopes and that the soil water and fertilizer resources obtained by the roots are not sufficient to support the aboveground parts to produce more carbohydrates and invest in underground roots [32]. It is also reported that fine root production and turnover in shrubs and forest trees growing in nutrient-poor karst ecosystems are higher and faster at upper slopes than at lower slopes [33]. Morphological changes in the driving root are closely related to changes in its internal anatomical structure [34]. In this study, there was no significant difference in the anatomical structural characteristics of the cross-section of the grades 1–3 roots of Chinese fir at different slope positions, but the thickness of the cortex of the 3rd order roots on the upper slope was the largest, the diameter of the vascular bundles and the ratio of the third-order roots at the middle slope were the largest, and the ratio of the second-order roots on the lower slope was the largest. From the perspective of anatomical structure, the third-order roots of Chinese fir at the middle slope and the second-order roots of Chinese fir at the lower slope have stronger transport capacities, whereas the third-order roots at the upper slope have a stronger ability to absorb nutrients and water [35].

The evolution of root anatomical characteristics may make the roots more efficient in terms of resource acquisition. For example, increasing the colonization of mycorrhizal fungi in the cortex can make root exploration of resources more efficient [36]. A larger cell size can reduce the cost of root construction, and the formation of cortical tissue is conducive to the storage of nonstructural carbon or compounds required for chemical defense [37,38]. The relationship between the anatomical structure and function of more than 500 plant roots in tropical, subtropical, and temperate forests revealed that the root structure of woody plants is limited by the development of anatomical structures. In

particular, during the transformation from root absorption capacity to transport capacity, primary tissues, including the cortex, age during the development of the cork plug layer and cell wall thickening, and additional sub-lignin deposition in the roots occur [39]. This, in turn, affects the accumulation of tissue chemical elements and changes the rate of root decomposition. The higher the degree of fine root lignification, the higher the carbon content, but the slower the decomposition rate [35,40]. In the present study, the contents of nitrogen and phosphorus in grades 1–3 Chinese fir roots showed the order of lower slope > middle slope > upper slope, but the C/N and C/P ratios showed the opposite trend. This indicates that the metabolic rate of the grades 1–3 roots of Chinese fir at the lower slope was higher than that of the roots at the upper and lower slopes, and the turnover rate of their production and death was faster [41]. The higher phosphorus content in the root tissues may be related to the physiological supplementation strategy obtained by increasing nutrient availability through root exudates and respiration during rapid turnover [42]. It was also found that the phosphorus content of fine roots increased with the decrease in slope position in *Tectona grandis* L. f. plantations [43]. This confirms our first hypothesis that the fine roots of Chinese fir change their morphology, anatomy, and chemical properties through plasticity changes and jointly construct a life strategy for efficiently absorbing the limited resources in soil under different slope positions.

4.2. Slope Position Drives the Changes in the Intrinsic Relationships of Fine Root Traits of Chinese Fir

The strategy of acquiring soil resources formed during root adaptation to changes in the environment is achieved through a series of fine root trait combinations [44]. The combination of multiple traits determines the life-history strategy for root survival. The coordination or trade-off relationships between different traits allows fast- or slow-growing roots to develop corresponding ecological strategies to adapt to resource-poor environments [23]. In the present study, there was a negative correlation between the diameter of the fine roots of Chinese fir and the specific root length, indicating that the fine roots of Chinese fir had the outsourcing strategy from mycorrhizal fungi to obtain resources, that is, a “collaborative dimension” [36]. In addition, root diameter, vascular bundle diameter, cortical thickness, and histochemical traits were negatively correlated, whereas specific root length was positively correlated with nitrogen and phosphorus contents. This is consistent with the conclusion that there is a negative correlation between root morphology and chemical traits under the assumption of fine root economic spectrum, indicating that the strategy of fine root absorption and utilization of Chinese fir follows the resource acquisition–utilization conservative trade-off one-dimensional root economic spectrum [45]. This reflects the trade-off between the resource acquisition efficiency and maintenance costs of Chinese fir roots. Simultaneously, fine roots optimize the allocation of resources between different functional traits, that is, the trade-off strategy [46].

The present study found that, in the process of adapting to different soil water and fertilizer resources, the most common relationship between root traits is the resource trade-off relationship that optimizes the allocation of limited available resources [47]. In this study, the root diameter at different slope positions was negatively correlated with specific root length; however, the vascular bundle diameter and cortical thickness at different slope positions were positively correlated with nitrogen content, whereas the root diameter of the upper slope was positively correlated with nitrogen content. This is beyond the scope of the resource trade-off strategy relationship between the acquisition–conservative axis in the root economic spectrum [45]. Kong et al. [48] analyzed the relationships between the anatomical, morphological, and chemical traits of more than 800 plant-absorbing roots and found that the relationships between root traits among species were mostly nonlinear owing to the allometric growth relationship between anatomical traits (cortex thickness and stele diameter). When Kong et al. [49] further divided fine roots (diameter ≤ 2 mm) into absorbing roots ($<247 \mu\text{m}$) and coarse absorbing roots, it was found that roots with larger diameters were more dependent on mycorrhiza when acquiring nutrients. The

relationship between these functional root traits does not support a resource trade-off strategy in the economic spectrum of fine roots [4]. Han et al. [5] used 20 tree species from the Puer subtropical monsoon evergreen broad-leaved forest in Yunnan, China, as research objects to explore the relationships between root physiological traits (phosphatase activity) and morphological and chemical traits, and for the first time revealed the cooperative dimension of fine root phosphatase activity in the economic space of fine roots, which is an active strategy for plants to obtain soil phosphorus.

These results indicate that in the root trait economic space, there are also multidimensional root trait economic space trade-off dimensions, such as the two-dimensional root trait economic space, in addition to classical conservative and collaborative dimensions [36]. Considering the changes in soil water and fertilizer resources for the growth of Chinese fir roots under different slope positions, the relationship between the morphological, anatomical, and chemical traits of Chinese fir may have multiple variation dimensions under different slope positions as well as a single acquisition and conservative resource trade-off relationship. This verifies our second hypothesis: that is, there is a clear trade-off between the function of root traits and mycorrhizal fungi in temperate and tropical tree species [50,51]. As symbionts in the interaction between roots and soil fungi, mycorrhizae play an important role in the formation of trade-off strategies for fine roots when obtaining soil resources [52]. With the help of mycorrhizal fungi, roots can obtain resources 'by themselves' or 'by outsourcing' to mycorrhizal fungi, thus adopting the resource acquisition–utilization conservative strategy [53]. Therefore, the formation of multiple dimensions of variation in the fine roots of Chinese fir under different slope positions may be related to mycorrhizal colonization [51].

5. Conclusions

The morphology, anatomy, and chemical properties of the fine roots of Chinese fir at different slope positions changed significantly due to root plasticity. By adjusting fine root traits, Chinese fir growing at the upper slopes can improve the absorption and utilization efficiency of soil resources by increasing the diameter of the grades 2–3 roots and the thickness of the cortex. Chinese fir growing at the middle slope pays attention to the construction of two to three levels and seeks to absorb soil resources by increasing the root length per unit of dry matter mass. Chinese fir growing at the lower slopes increased the root absorption area and length per unit mass by increasing investment in first-order root biomass to obtain limited resources via absorption. The foraging strategy of Chinese fir fine roots at the upper slope was biased toward resource conservation through synergistic changes in the fine root traits. On the other hand, the foraging strategy of the fine roots at the middle and lower slopes was biased toward resource acquisition. Therefore, continuous monitoring of changes in fine root traits is crucial for improving the productivity of Chinese fir plantations. However, there is still a wide range of competitive possibilities among the different fine root traits. Some important tradeoffs limit the types of competitive trait combinations in fine roots. Further research on the intrinsic relationships between multiple fine root traits is required to combine physiological and biological traits.

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