

Article

Effects of Tree Species on Moso Bamboo (*Phyllostachys edulis* (Carriere) J. Houzeau) Fine Root Morphology, Biomass, and Soil Properties in Bamboo–Broadleaf Mixed Forests

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Abstract: Understanding fine root characteristics in relation to soil properties of bamboo–broadleaf mixed forests may help optimize belowground production management and ecological functions in mixed-forest ecosystems. In this study, we compared four different bamboo–broadleaf mixed forests: *Castanopsis chinensis* (Sprengel) Hance with moso bamboo (CCB), *Alniphyllum fortunei* (Hemsl.) Makino with moso bamboo (AFB), *Choerospondias axillaris* (Roxb.) Burt and Hill with moso bamboo (CAB), and *Castanopsis fargesii* Franch with moso bamboo (CFB), and analyzed their effects on the traits of fine roots of moso bamboo, soil nutrient contents, and enzyme activities. In January 2022, fine root and soil samples from four different mixed bamboo–broadleaf forests were collected from a subtropical region of Fujian Province, China. Results showed that CAB significantly increased fine root biomass (FRB) and root length density (RLD); however, specific root length (SRL) was only in the 0–20 cm soil layer. Specific surface area (SSA) was significantly reduced in the CCB in the 0–20 cm and 20–40 cm soil layers. The total phosphorous (TP) and total potassium (TK) contents of AFB and CAB were significantly increased ($p < 0.05$), and the alkali-hydrolyzable nitrogen (AN) content was significantly increased by CCB in the 0–20 cm soil layer ($p < 0.05$). Additionally, CFB increased the activities of acid phosphatase (ACP) and catalase (CAT) but decreased the activity of sucrase (SC). Principal component analysis showed that fine root traits (FRB, RLD, SRL, and SSA) were not only positively associated with soil organic carbon (SOC), total nitrogen (TN) and available potassium (AK) but also associated with urease (UE) and CAT. Therefore, belowground interactions between different species have a significant impact on the characteristics of fine roots and soil in bamboo–broadleaf mixed forests.

Keywords: moso bamboo; broadleaf mixed forest; fine root plasticity; soil nutrients; soil enzyme activity



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1. Introduction

Mixed forests are composed of two or more species, which can positively affect above- and belowground ecosystem properties and processes and have been proposed as a forest management strategy to resist and adapt to environmental changes compared to far-from-nature monocultures [1,2]. It emphasizes the interactions of ecological features of species as a condition for achieving maximum ecological advantages [3]. At present, there is a hypothesis that explains the advantages of mixed forests: the complementarity effect, which refers to positive interspecific interactions such as reduced competition, easier resource capture, and better growth conditions [4]. However, our current understanding of the effects of species composition and interspecific interactions in mixed forests is primarily based on aboveground component research [5–7]. Belowground factors and their interactions have received far less attention [8,9].

Fine roots (diameter ≤ 2.0 mm) are crucial vegetative organs of plants that enable material exchange and energy flow in the aboveground environment [10]. Plants can detect and distinguish their neighbors through fine roots and adjust their nutrient exploitation strategies accordingly [11,12], especially when confronted with belowground competition for soil resources between species [13]. The capacity of plants to absorb nutrients is determined by fine root traits, such as acclimatization by altering fine root biomass allocation and morphology, which are key indicators of plant growth to ensure survival [14]. For example, the production of fine roots significantly contributes to carbon and nutrient cycling in forest ecosystems [15]. Specific root length (SRL) is generally regarded as the efficiency of roots to proliferate in soil per unit of carbon invested in prospective nutrient uptake ability [16,17], and root tissue density (RTD) is also used to evaluate the absorptive potential and turnover of fine roots [18]. In addition, the activity of soil enzymes may help understand plastic fine root responses to resource availability for plants and microbes to degrade complex organic substances and make nutrients available for root uptake [19,20]. Previous findings have demonstrated that fine root traits may follow a similar conservation/acquisition trade-off [21]. Resource-acquisitive fine roots have high SRL and low RTD, whereas resource-conservative roots have high RTD and low turnover [21]. However, it is unclear whether different strategies for the exploitation of belowground resources exist between tree species and other plant guilds, such as moso bamboo.

China has about 6.41 million hectares of bamboo forest, which is home to over 534 species in 34 genera, and accounts for 20% of the world's bamboo forest area [22]. Moso bamboo (*Phyllostachys edulis* (Carrière) J.Houz.) has a unique feature in that it grows 30–100 cm each day during its peak growth stages after sprouting and consequently has become a valuable bamboo species [23,24]. Although the mixing of broad-leaved forest tree species with moso bamboo has been widely used in China, mixed species need to be matched appropriately to improve the belowground stability and productivity of the ecosystem [25–27]. Thus far, less attention has been paid to belowground processes between species than to their aboveground counterparts in bamboo–broadleaf mixed forests [28].

Understanding how interspecies interactions alter underground ecological processes can not only elucidate the factors that drive productivity changes in mixed-species stands but may also contribute to a broader understanding of community ecology. In a broader sense, this knowledge is critical for the future development of sustainable production systems. Research on the adaptability of mixed stands with different species compositions should assist in regulating forest ecosystems. The morphological distribution patterns of underground fine roots under diverse growth environmental conditions should clarify the regulatory mechanisms of roots in stands, and they should be useful in guiding management plans and boosting forest production. Thus, this study was conducted in four different mixed broadleaf tree species and moso bamboo in the Tianbaoyan Nature Reserve to (1) reveal the plasticity response and characteristics of moso bamboo fine roots and (2) explore the influence of tree species differences on the fine root and soil characteristics of moso bamboo–broadleaf mixed forests.

2. Materials and Methods

2.1. Site Description

This study was conducted at the Tianbaoyan National Nature Reserve (25°50'51"–26°01'20" N, 117°28'03"–117°35'28" E, Fujian Province, China). (Figure 1). The area is characterized by a mid-subtropical marine monsoon climate, with an annual average temperature of 15 °C (min. and max. are –11 °C and 40 °C, respectively) and precipitation of 2039 mm, with an annual average relative humidity >80% and an annual average frost-free period of approximately 290 days. This region is dominated by middle and low mountains at 580–1604.8 m a.s.l., where the main type of soil is subsoil accumulation of humus and/or oxides [29,30]. Moso bamboo is a fast-growing shade-tolerant species with high economic value in this region. The main evergreen tree species with Moso bamboo were *Castanopsis chinensis* (Sprengel) Hance and *Castanopsis fargesii* Franch., and the deciduous tree species

were *Alniphyllum fortunei* (Hemsl.) Makino, and *Choerospondias axillaris* (Roxb.) Burtt et Hill. In 1996, the Chinese government designated the study area as a nature reserve; therefore, managers only harvested moso bamboo that had matured for 5–6 years in mixed bamboo–broadleaf forests.

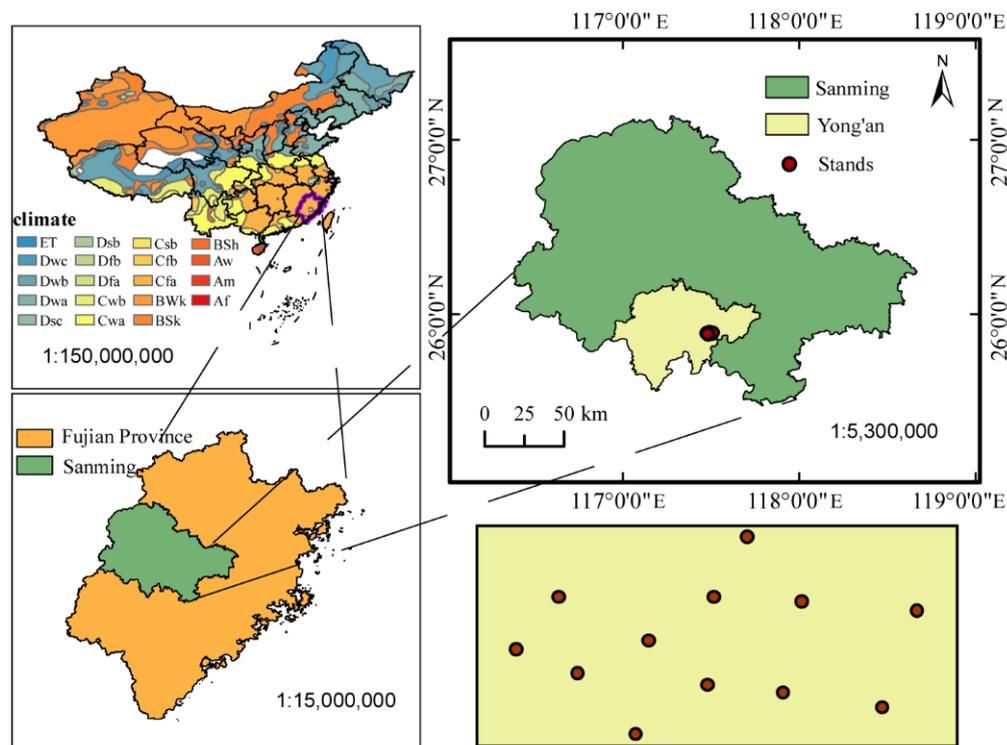


Figure 1. The geographic location of the study site.

2.2. Experiment Design

In January 2022, field experiments were conducted in accordance with the overall exploration of mixed forests in protected areas. A mixed forest of bamboo and broadleaf trees was selected under the same site conditions (Table 1). We used typical sampling methods to set up four different bamboo–broadleaf mixed forests: *Castanopsis chinensis* with moso bamboo (CCB), *Alniphyllum fortunei* with moso bamboo (AFB), *Choerospondias axillaris* with moso bamboo (CAB), and *Castanopsis fargesii* with moso bamboo (CFB), and took a broadleaf tree as the center with a radius of 9 m (Figure 2). In total, 12 sample stands were established. To reduce spatial autocorrelation, each stand type was replicated in three spatially interspersed stands at distances > 300 m [31]. The stand’s boundary was 100 m from the forest edge bordering either agricultural land or roads, ensuring that there were no other broadleaf trees in the circular sample stand apart from moso bamboo.

Table 1. Stand characteristics of bamboo–broadleaf mixed forests.

Stand Type	Age of Broadleaf Tree (a)	DBH of Broadleaf Tree (cm)	Average DBH of Bamboo (cm)	Culm Density (culm ha ⁻¹)	Altitude (m)	Slope (°)	Aspect
CCB	53	40.82	8.89	2829	796	20	adret
AFB	55	49.11	9.15	2712	770	25	adret
CAB	44	41.36	9.48	2868	778	22	adret
CFB	56	53.55	9.37	2987	789	23	adret

Note: Bamboo–broadleaf mixed forests: *Castanopsis chinensis* (Sprengel) Hance with moso bamboo (CCB), *Alniphyllum fortunei* (Hemsl.) Makino with moso bamboo (AFB), *Choerospondias axillaris* (Roxb.) Burtt and Hill with moso bamboo (CAB), and *Castanopsis fargesii* Franch with moso bamboo (CFB).

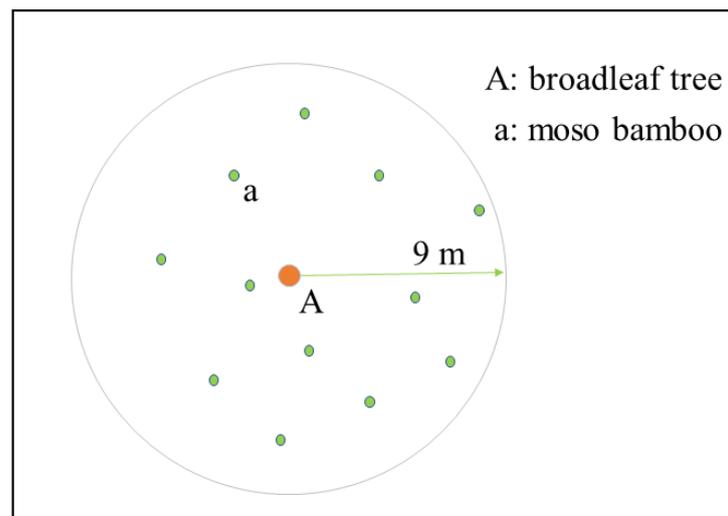


Figure 2. Schematic diagram of stands.

2.3. Fine Root Sampling and Analysis

We used soil coring (50 mm diameter, 20 cm height) to collect fine roots of Moso bamboo in early January 2022, when growth was slow [32]. In the sample stand, nine sampling points were randomly selected and separated into three layers: 0–20, 20–40, and 40–60 cm, comprised almost entirely of fine roots [33]. The samples were brought back to the laboratory, and the roots and soil were placed in a soil sieve (aperture size = 2.0 mm) to separate impurities, such as soil, gravel, and dead leaves. The separated roots were then placed in a sieve with a pore diameter of 0.85 mm. The sediment attached to the fine roots was washed with running water, the washed root was laid flat on the surface of the evaporating dish, and the roots of the Moso bamboo were carefully selected and graded with tweezers, Vernier calipers, and a magnifying glass (diameter ≤ 2 mm). Live and dead roots were identified according to their configuration, color, and elasticity. In this study, a root with a diameter ≤ 2 mm was defined as a fine root [33]. Fresh roots were weighed using an electronic scale (0.0001 g) and scanned using a ScanMaker i800 scanner, and photos were saved as JPEG files (300 dpi). The root analysis system (WSeen's Root Analysis System, model_LA-S, China) was used to analyze root length (RL, cm) and surface area (RSA, cm^2). The roots were then oven-dried at 65 °C to a constant weight to calculate root dry mass (RDM, g). Specific root length (SRL, $\text{cm}\cdot\text{g}^{-1}$) and specific surface area (SSA, $\text{cm}^2\cdot\text{g}^{-1}$) reflect morphological and physiological functions. Root length density (RLD, $\text{m}\cdot\text{m}^3$) is a significant indicator of fine root nutrient and water absorption capacity. Fine root biomass (FRB, $\text{g}\cdot\text{m}^3$), SRL ($\text{m}\cdot\text{g}^{-3}$), and RLD ($\text{m}\cdot\text{m}^{-3}$) were calculated using the following equations [33]:

$$\text{SRL} = \text{RL}/\text{RDM} \quad (1)$$

$$\text{SSA} = \text{RSA}/\text{RDM} \quad (2)$$

$$\text{FRB} = \text{RDM} \times 10^6 / [\pi(d/2)^2 \times h] \quad (3)$$

$$\text{RLD} = \text{RL} \times 10^6 / [\pi(d/2)^2 \times h] \quad (4)$$

where d is the diameter (cm) and h is the height (cm) of the core.

2.4. Soil Sampling and Analysis

In January 2022, nine soil cores were sequentially extracted from each stand by soil coring. The sampling depths were 0–20 cm, 20–40 cm, and 40–60 cm. The corings from the same layer were combined to form a composite sample. After removing coarse roots from the mixed samples using a 2 cm sieve, the chemical characteristics of the soil were measured after air-drying. An elemental analyzer (Costech ECS 4024 CHNSO, Picarro, Italy) was used

to determine the soil organic carbon (SOC) and total nitrogen (TN) content. Using an automatic chemical analyzer, the total phosphorus (TP) content of the soil was determined using the molybdenum–antimony resistance colorimetric method (concentrated $\text{H}_2\text{SO}_4\text{--HClO}_4$) (Smartchem 300, AMS, Corsico, Italy). The total potassium (TK) content of the soil was determined using a flame photometer (M410; Sherwood, UK). The alkali-hydrolyzable diffusion method was used to determine the alkali-hydrolyzable nitrogen content (AN) of the soil. Available soil phosphorus (AP) content was determined using a continuous flow analyzer (AA3, Seal, Norderstedt, Germany). Flame atomic absorption spectrometry was used to determine the amount of available potassium (AK). Soil sucrose (SC) was determined by the 3,5-dinitrosalicylic acid colorimetric method. Urease (UE) activity was determined using the phenol-sodium hypochlorite colorimetric method, acid phosphatase (ACP) was determined using the phenyldisodium phosphate colorimetric method, and catalase (CAT) was determined using the potassium permanganate titration method.

2.5. Data Analysis

One-way analysis of variance (ANOVA), LSD, and Duncan's test were used to detect significant differences ($\alpha = 0.05$) between fine root traits, biomass, and soil properties in the four stand types. Homogeneous variance and assumptions of normality were examined using the Leven test and Shapiro–Wilk test, respectively. Principal component analysis (PCA) was used to examine the associations between fine root traits and soil properties. The PCA was calculated with the 'FactoMineR' package. Graphs were drawn with the 'ggplot2' package. All statistical analyses were performed using SPSS 25.0 and collated using Excel 2019, and all figures were created using OriginPro 2017C SR2b9.4.2.380 (Northampton, MA, USA) and RStudio (Version 1.3.1093).

3. Results

3.1. Fine Root Traits

FRB and RLD significantly decreased with increasing soil depth in the four mixed bamboo–broadleaf forests (Figure 3, $p < 0.05$). CAB significantly increased FRB and RLD compared with CCB and CFB in the 0–20 cm and 40–60 cm soil layers, but for SRL, it was only in the 20–40 cm soil layer ($p < 0.05$). However, there was no significant difference between AFB and CFB in SRL and RLD. CCB significantly decreased SSA in the 0–20 cm and 20–40 cm soil layers ($p < 0.05$).

3.2. Soil Properties

SOC, AN, and AP content significantly decreased with increasing soil depth in the four stand types (Table 2, $p < 0.05$). Compared with CCB and CFB, AFB and CAB significantly increased the content of TP and TK in the 0–20 cm and 20–40 cm soil layers ($p < 0.05$). Meanwhile, the content of SOC, TN, and AK was significantly increased by CAB in the 0–20 cm and 20–40 cm soil layers. The AN content of CCB significantly increased in the 0–20 cm soil layer ($p < 0.05$).

3.3. Soil Enzyme Activity

The activity of CAT significantly decreased with increasing soil depth in CCB and CFB (Figure 4, $p < 0.05$). AFB and CAB significantly increased the activity of SC and reduced the activity of ACP in the 20–40 cm soil layer. AFB significantly increased UE activity in the 0–20 cm soil layer. The CAT activity of CFB was significantly increased in the three soil layers ($p < 0.05$).

3.4. Associations between Stand Fine Root Traits and Soil Properties

A PCA of fine root traits and soil properties explained 74.1% of the first two principal axes (Figure 5). The first PCA axis explained 59.3% of the variance and was mainly represented by RLD (10.74%), AN (10.42%), and SRL (9.89%), whereas the second PCA axis explained an additional 14.8% of the variance and was associated primarily with ACP

(29.51%), TK (26.89%), and UE (11.17%) (Table 3). The fine root traits were significantly positively correlated with soil enzymes (i.e., UE and CAT) and SOC, TN, and AK, but did not show correlations with TK. ACP was negatively correlated with TN and TK, and no significant correlations were seen with fine root traits.

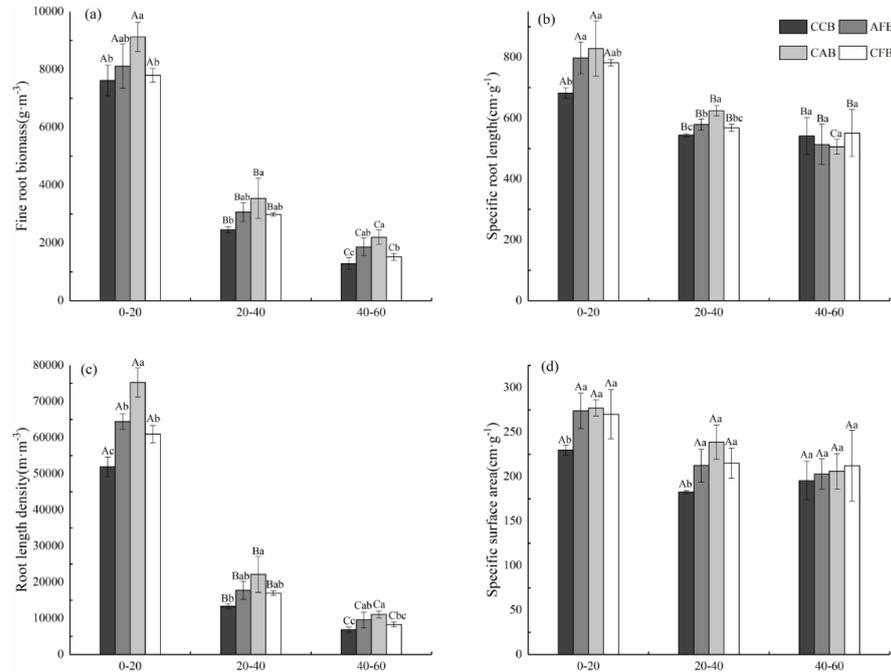


Figure 3. (a) Fine root biomass, (b) specific root length, (c) root length density and (d) specific surface area in mixed forest of bamboo–broadleaved trees. Error bars indicate the standard deviation ($n = 3$). Capital letters indicate the difference in fine root characteristics between different soil layers under the same stand ($p < 0.05$); lowercase letters indicate differences in fine root characteristics between different stands in the same soil layer ($p < 0.05$).

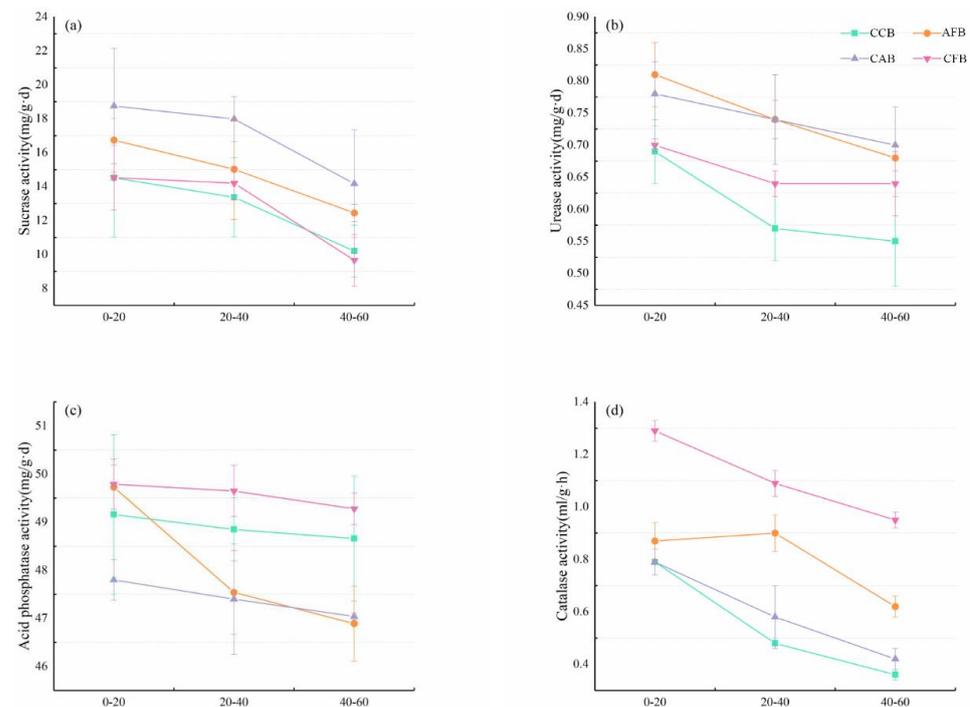


Figure 4. (a) Sucrase activity, (b) urease activity, (c) acid phosphatase activity and (d) catalase activity in mixed forest of different bamboo and broad-leaved trees.

Table 2. Soil characteristics for different bamboo–broadleaf mixed forests.

Stand Type	Soil Layer cm	SOC (g/kg)	TN (g/kg)	TP (g/kg)	TK (g/kg)	AN (mg/kg)	AP (mg/kg)	AK (mg/kg)
CCB	0–20	30.38 ± 1.03 Ab	2.12 ± 0.10 Ac	0.33 ± 0.01 Ab	12.99 ± 2.39 Ac	144.91 ± 2.34 Aa	1.69 ± 0.17 Ad	32.77 ± 2.68 Ab
	20–40	23.43 ± 2.78 Bab	1.87 ± 0.05 Bb	0.30 ± 0.01A Bc	13.25 ± 0.82 Ad	114.89 ± 5.45 Ba	0.88 ± 0.05 Bc	21.97 ± 4.32 Bb
	40–60	14.93 ± 0.83 Ca	1.84 ± 0.12 Ba	0.29 ± 0.03 Ba	12.67 ± 1.53 Ad	101.73 ± 3.19 Ca	0.13 ± 0.02 Cab	18.44 ± 3.70 Bb
AFB	0–20	34.66 ± 2.52 Ab	2.49 ± 0.24 Ab	0.39 ± 0.01 Aa	36.27 ± 4.56 Aa	127.99 ± 1.16 Ab	3.71 ± 0.10 Aa	45.97 ± 5.88 Aab
	20–40	24.30 ± 2.51 Bab	1.93 ± 0.15 Bab	0.39 ± 0.03 Aa	37.08 ± 3.53 Aa	105.05 ± 2.76 Bab	1.24 ± 0.09 Ba	36.18 ± 2.22 Ba
	40–60	17.10 ± 1.30 Ca	1.84 ± 0.07 Ba	0.30 ± 0.02 Ba	37.48 ± 4.41 Aa	85.61 ± 1.20 Cc	0.15 ± 0.01 Cab	17.69 ± 1.23 Cb
CAB	0–20	46.71 ± 7.53 Aa	2.81 ± 0.11 Aa	0.39 ± 0.01 Aa	29.13 ± 3.27 Ab	127.93 ± 1.45 Ab	3.44 ± 0.09 Ab	54.39 ± 12.25 Aa
	20–40	27.19 ± 3.25 Ba	2.17 ± 0.21 Ba	0.36 ± 0.01 Bb	28.54 ± 2.79 Ab	105.09 ± 6.98 Bab	1.11 ± 0.14 Bab	43.27 ± 4.29 ABa
	40–60	17.29 ± 1.86 Ca	1.83 ± 0.17 Ca	0.27 ± 0.01 Cab	29.29 ± 3.46 Ab	90.92 ± 2.59 Cb	0.17 ± 0.03 Ca	28.9 ± 3.35 Ba
CFB	0–20	30.23 ± 1.77 Ab	2.26 ± 0.18 Abc	0.28 ± 0.01 Ac	19.88 ± 4.31 Ac	104.25 ± 7.09 Ac	2.07 ± 0.05 Ac	35.66 ± 0.62 Ab
	20–40	20.05 ± 1.30 Bb	1.95 ± 0.08 Bab	0.27 ± 0.01 Ac	21.12 ± 4.21 Ac	94.82 ± 6.81 Bb	1.03 ± 0.04 Bbc	24.17 ± 6.24 Bb
	40–60	16.06 ± 0.61 Ca	1.80 ± 0.08 Ba	0.24 ± 0.02 Bb	20.96 ± 4.00 Ac	82.07 ± 1.89 Cc	0.12 ± 0.02 Cb	29.93 ± 1.62 ABa

Values are presented as the mean ± standard deviation (n = 3). Different lowercase letters indicate significant differences between different stands in the same soil layer; different capital letters indicate significant differences between different soil layers in the same stand (one-way ANOVA and LSD test, $p < 0.05$). SOC: soil organic carbon; TN: total nitrogen; TP: total phosphorus; TK: total potassium; AN: alkali-hydrolyzable nitrogen; AP: available phosphorus; AK: available potassium.

Table 3. Principal component analysis contribution rate of variables.

	FRB	SRL	RLD	SSA	SOC	TN	TP	TK	AN	AP	AK	SC	UE	ACP	CAT
Dim. 1	9.8908	9.2673	10.0738	7.7663	9.7735	9.0609	5.7811	0.8213	10.4241	5.6534	8.1469	5.3079	5.7967	0.2791	1.9562
Dim. 2	2.5446	2.6883	2.4592	0.1151	0.0410	0.0067	6.6185	26.8863	0.3373	2.2351	2.4934	5.5981	11.1667	29.5147	7.2946

Note: SRL, specific root length; SSA, specific surface area; RLD, root length density; FRB, fine root biomass; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, alkali-hydrolyzable nitrogen; AP, available phosphorus; AK, available potassium; SC, sucrose; UE, urease; ACP, acid phosphatase; CAT, catalase.

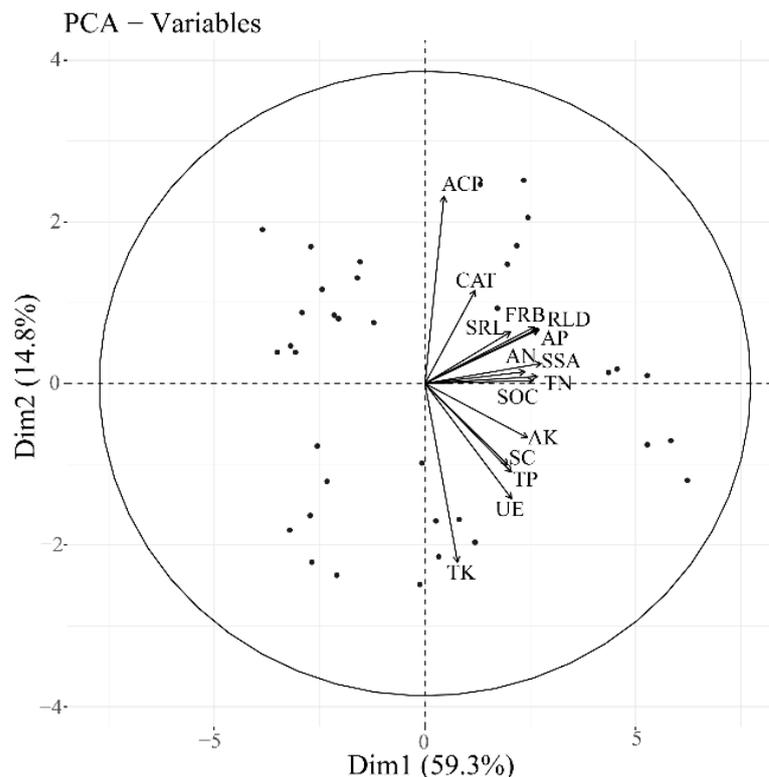


Figure 5. Principal component analysis of variables. The arrow line of the variables is plotted as the correlation coefficients between them and the first two principal components in the unit circle; the length of the arrow line indicates the contribution of the variable.

4. Discussion

Fine root traits represent essential trade-offs between resource acquisition and costs [34]. In this study, CAB significantly increased the FRB of moso bamboo (Figure 3, $p < 0.05$), but the biomass decreased significantly with soil depth, which is consistent with the results of Yuan and Miao [35,36]. The change in biomass allocation when clonal plants (Moso bamboo) adapt to the environment is an important biological characteristic of plant-coordinated growth [37]. Plants can adjust their rooting depths and grow fine roots in soil layers with more resources or less root competition [38]. The possible reasons for the increase in FRB are as follows: first, *Choerospondias axillaris* is a deep-rooted plant, and moso bamboo is a shallow-rooted plant that avoids direct competition for soil nutrients or water [39], so the bamboo spreads its fine roots into the more nutrient-rich topsoil; and second, the abundant litter of *Choerospondias axillaris* may be brought into the soil by leaching, which promotes the ability of the fine roots to obtain nutrients from the soil surface. Various studies have concluded that a reduction in SRL can help plants adapt to competitive pressures. For example, Lai et al. [40] found that wheat increased RLD and decreased SRL in a walnut-wheat agroforestry system. Zamora et al. [41] also found that SRL was significantly reduced in competition between *Gossypium hirsutum* L. and *Carya illinoensis* (Wangenheim) K. Koch. However, some scholars have proposed that an increase in SRL is conducive to enhancing fine-root competitiveness [42]. Curt and Prévosto [43] found the SRL of *Quercus glauca* Thunb. improved root competition with *Pinus sylvestris* and *Betula pendula* Roth. In our study, we found that CAB significantly increased SRL and RLD in the 0–20 cm soil layer, and CCB significantly decreased SSA in the 0–20 cm and 20–40 cm soil layers (Figure 3, $p < 0.05$). This may be because, to obtain more nutrient resources and gain an advantage in the competition, allelopathic substances in root exudates have intentional or harmful allelopathic effects on other plants, such as affecting nutrient availability in soil or microbial activities and affecting root morphology and growth. Using principal component analysis, we found that fine root biomass and morphological characteristics

(SRL, RLD, and SSA) were strongly positively correlated with SOC, TN and AK (Figure 5), which is consistent with the results of Zheng [44]. This suggests that soil properties can significantly influence root characteristics. Therefore, we can speculate that a higher level of soil nutrients induces root extension to a greater soil depth, which in turn stimulates root growth and proliferation.

Different tree species have a strong influence on the chemistry of forest soils [45]. We conclude that soil nutrients were affected by different mixed tree species, and SOC content was significantly higher than in other stand types in CAB (Table 2, $p < 0.05$). Miller H G. [46] reported that differences in species growth rate and litter characteristics also affect the rate of litter decomposition, leading to the accumulation of organic matter. Wang [47] has suggested that the presence of N-fixing species may accelerate litter decomposition to increase soil organic C. Both are likely to explain why the rate of litter decomposition of *Choerospondias axillaris* was faster than other species, resulting in a greater accumulation of soil organic matter in the stands [48]. In addition, AFB and CAB significantly increased the content of TP and TK in the 0–20 cm and 20–40 cm soil layers, and the AN content of CCB was significantly increased in the 0–20 cm soil layer (Table 2, $p < 0.05$). Zhang [49] suggested that different canopy proportions in the bamboo–broadleaf mixed forest could influence the soil's physical and chemical properties of the forest. The difference in canopy structure or light transmittance of broadleaf trees results in differences in soil temperature and humidity in the forest, affecting soil microbial activities and changing the conversion rate of available soil nutrients. Thus, different tree species may result in variations in microbial community composition, which may affect the local carbon and nutrient pools and fluxes.

Soil enzymes play important roles in nutrient cycle processes and the maintenance of soil health [50]. The composition of various plant life forms helps increase enzyme activity in the soil [51,52]. Avazpoor Z. and Masayuki Ushio [53,54] showed that the soil enzyme activities varied with the different species, with better soil aeration and higher litter input by trees at the soil surface and topsoil layers compared to the subsoil [55]. The fact that the sources of soil enzymes are primarily animal and plant residues, microbial activities, and plant root exudates, whereas the surface soil has many roots, good aeration, rich accumulation of various substances, and numerous biological species and quantities [52]. This may explain why the activity of CAT gradually decreased with increasing soil depth in CCB and CFB (Figure 4, $p < 0.05$). Generally, deciduous broad-leaved trees generate more litter than evergreen broad-leaved trees. Microorganisms in deciduous tree with moso bamboo mixed forests allocate more resources to soil enzyme production and improve soil fertility to meet the demands of plant and microbe growth [56]. These factors may contribute to the high SC and UE activity observed in AFB and CAB (Figure 4, $p < 0.05$). Likewise, an increase in soil catalase activity may alter soil solution chemistry and redox conditions. These changes in the soil solution can dissociate metal–metal connections and complex organic matter bonds, altering soil carbon storage [47]. CFB had a much higher CAT activity than the other stand types in all three soil layers (Figure 4, $p < 0.05$). Therefore, we speculated that the high value of CAT activity in CFB indicated that *Castanopsis fargesii* played a significant role in changing soil redox, resulting in improved soil saprophytic intensity and organic matter accumulation, increased soil removal ability for harmful substances and enhanced tree resistance. Moreover, further studies should be conducted on the composition of root exudates, understory vegetation diversity, and light environments to confirm these speculations.

5. Conclusions

Our research indicates that the fine root morphological plasticity of moso bamboo and the enzyme and chemical properties of the soil in bamboo–broadleaf mixed forests differ as the mixed tree species changes in a stand. AFB and CAB significantly stimulated root growth and morphological changes of Moso bamboo for more rapid soil exploration. AFB significantly increased the content of TP and TK in the 0–20 cm soil layer but reduced

the activity of ACP in the 20–40 cm soil layer. ACB not only increased FRB and RLD in the 0–20 cm soil layer but also increased SC activity in the 0–20 cm soil layer. There is a correlation between fine root traits (FRB, RLD, SRL, and SSA) and enzymes (UE and CAT) and nutrients (SOC, TN, and AK) in soil. The changes in fine root traits may be caused by increasing litter quality, soil conditions and biological activities. Further research should address these points. Although our study did not exclude the errors associated with other environmental factors, it can provide a theoretical basis for the local, sustainable management of bamboo–broadleaf mixed forests.

Author Contributions: F.G. designed this study and improved the English language and grammar. Y.Z. (Yang Zhou) wrote the first draft of the manuscript and performed data analysis. Y.Z. (Yang Zhou) and Z.L. performed fieldwork. Y.Z. (Yaxiong Zheng), X.Z. (Xiao Zhou) and X.Z. (Xuan Zhang) provided guidance and methodological advice. All coauthors contributed to the discussion, revision, and improvement of the manuscript. All authors have read and agreed to the published version of the manuscript.

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