

Bamboo Expansion Affects the Vertical Distribution and Phenotypic Plasticity of Root Systems of Native *Cunninghamia lanceolata* and Expanding *Phyllostachys edulis* in Middle-Southern China

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Bamboo Expansion Affects the Vertical Distribution and Phenotypic Plasticity of Root Systems of Native *Cunninghamia lanceolata* and Expanding *Phyllostachys edulis* in Middle-Southern China

Abstract: Bamboo expansion is widely recognized as a major driver of declining native biodiversity; however, the belowground interactions between expanding bamboo and native tree species remain poorly understood. In this study, we investigated the differences between the expanding species *Phyllostachys edulis* (*Pe*) and the native species *Cunninghamia lanceolata* (*Cl*) in terms of vertical root biomass distribution and the phenotypic plasticity of different root orders across various stages of bamboo expansion. Our results showed that as bamboo expansion intensified, *Cl* exhibited a notable reduction in root biomass density, particularly in the upper soil layers, coupled with increased root allocation in deeper layers. Concurrently, fine roots of *Cl* displayed significant increases in specific root length (SRL), root length density (RLD), and root specific surface area (RSA). In contrast, the rhizome-based root system of *Pe* remained relatively stable in biomass but exhibited significantly higher phenotypic plasticity indices for fine roots compared to *Cl*. Vertically, the two species showed clear root stratification, with *Pe* dominating the nutrient-rich upper soil layers, while *Cl* increasingly allocated fine roots to deeper layers. In mixed stands, *Cl* was consistently outcompeted by *Pe* in both spatial distribution and morphological plasticity, resulting in compromised nutrient acquisition. These findings provide mechanistic insight into how bamboo expansion alters belowground dynamics and contributes to the decline in native species, thereby reducing community biodiversity from a root system perspective.

Keywords: Bamboo expansion, root system interaction, vertical distribution, phenotypic plasticity, soil environment

1. Introduction

Root systems play a critical role in tree stability and in the uptake of nutrients and water (Gregory et al. 2017; Fontana et al. 2020; Pivovarovff et al. 2021). They also constitute a substantial portion of living dry-matter biomass (Huang et al. 2021). Due to belowground resource limitations, root systems have evolved a range of architectural and physiological responses to optimize nutrient acquisition (Wang et al. 2012). Species with highly plastic root systems often exhibit a competitive advantage in resource allocation, particularly under infertile soil conditions (Berntson and Wayne 2000; Cahill and Casper 2003). However, the duration and magnitude of this advantage may shift over time (Gruntman and Novoplansky 2004), potentially influencing both global carbon budgets and terrestrial ecosystem dynamics (Eissenstat et al. 2000). Thus, root systems have profound implications for plant growth and community evolution.

Belowground competition for resources is ubiquitous in natural ecosystems, yet it is a highly complex process (Rogers et al. 1994; Bais et al. 2006; Cahill et al. 2010; Hodge et al. 2009). Plant responses to neighboring roots depend on species-specific traits and the prevailing resource constraints (de Kroon et al. 2003; Magalhães et al. 2015). For instance, in karst regions characterized by severe soil and water erosion, shallow-rooted species may alter root biomass and growth patterns to maintain competitive advantage over deep-rooted counterparts (Zhao et al. 2017). Soil nutrient heterogeneity—driven by factors such as temperature, microbial activity, and atmospheric carbon dioxide concentration—strongly influences root morphology and spatial distribution. In nutrient-rich patches, plants increase root numbers and adjust fine root traits such as diameter, branching angle, internode length, and overall architecture to enhance nutrient uptake efficiency (Ding et al. 2018). Additionally, physiological responses can rapidly compensate for limited root biomass in varying soil conditions (Wang et al. 2015). However, some studies suggest that increased biomass allocation and nutrient content, rather than morphological changes, may be the primary adaptive strategy (Kramer-Walter et al. 2016, 2017; Wu et al. 2020). Therefore, it is critical to study root system competition in the context of the surrounding soil environment.

Bamboo is an important non-timber forest resource, but its expansion has been increasingly associated with adverse ecological impacts (Gaku et al. 2011; Montti et al. 2014; Peng et al. 2022). For example, Ying et al. (2016) reported a 4.7% decline in the carbon pool of evergreen broad-leaf forests in the Tianmu Mountain region over the past 30 years due to bamboo encroachment. Favorable conditions for

bamboo growth can alter soil physicochemical properties, microbial communities, and the lifespan of native vegetation (Fukushima et al. 2014; Li et al. 2017; Xu Q et al. 2019). These impacts can simplify community structure and reduce faunal biodiversity (Yoshifumi et al. 1998), thereby influencing successional dynamics. Bamboo's inflected rhizome system demonstrates exceptional resilience under resource-poor or disturbed conditions (Phillips et al. 2015; Lurie et al. 2017). These rhizomes respond to environmental stimuli and mechanical barriers, enabling them to penetrate rock fissures and expand their territory (Popova et al. 2016; Peng et al. 2021). Given the central role of rhizomes in bamboo expansion, understanding root-root interactions among competing species is essential. Although previous studies have examined bamboo root phenotypic plasticity (Shen et al. 2016; Qu et al. 2020), few have assessed root functional adjustments from both native and invasive perspectives.

Understanding the complex interactions and competitive strategies between bamboo and native root systems, particularly how functionally distinct roots adapt their traits and distribution, remains a significant challenge. This study aims to compare biomass density and phenotypic plasticity across root orders of *Phyllostachys edulis* (Pe, moso bamboo) and *Cunninghamia lanceolata* (Cl, Chinese fir) at varying stages of bamboo expansion. Specifically, our objectives were to: 1) Examine the competition for spatial soil resources between native and expanding root systems; and 2) Elucidate the functional allocation and adaptive strategies of root systems in both species in response to bamboo expansion.

2. Material and methods

2.1 Study area

The study was conducted at Wannian Forest Farm, situated at the southern end of Dawei Mountain National Forest Park in mid-southern Hunan Province, China (28°21'–28°22' N, 114°4'–114°5' E). The site experiences a humid subtropical monsoon climate, with an average annual temperature of 11–16 °C and annual precipitation ranging from 1800 to 2000 mm. The frost-free period extends for approximately 243 days. The hilly terrain exhibits slope gradients between 17° and 34°, with an average elevation of 603 m. The soil type is decomposed granite, typically yellow in color. Historical land-use practices, including the felling of broad-leaved trees and the planting of coniferous (Cl) trees in 1958, have led to the widespread establishment of Chinese fir forest stands. The preserved soil layer, with a rock content and depth ranging from 30 to 120 cm, reflects minimal anthropogenic disturbance. In recent years, reduced demand for timber has resulted in poor management of Chinese fir stands,

thereby facilitating the expansion of neighboring *Pe* (moso bamboo). The study site is managed by the Forestry Bureau of Changsha City. Field investigations complied with relevant Chinese regulations, and permission for plant root and soil collection was obtained from the landowner.

2.2 Experiment design and field investigation

Following a preliminary field survey, three mixed-species interfaces that had remained undisturbed by human activity for at least seven years were selected. Belt transects measuring 20 m × 60 m were established across these interfaces to capture variation across expansion gradients. Each transect was divided into three zones: a pure *Pe* forest stand, a mixed stand of *Pe* and *Cl*, and a pure *Cl* forest stand. To assess the effects of expansion over time, each belt transect was further divided into four sub-belts (5 m × 20 m), positioned at different distances along the expansion gradient (Figure 1). These sub-belts were classified as: (1) PES – *Pe* forest stand, (2) PCM – *Pe* forest stand with scattered *Cl* individuals, (3) CPM – *Cl* forest stand with scattered *Pe* shoots, and (4) CLS – pure *Cl* forest stand. Root and soil samples were collected along the direction of bamboo expansion.

2.3 Soil Sampling and Analysis

Within each sub-belt, ten soil profiles were randomly selected for root system sampling across depths of 0–80 cm, corresponding to the primary rooting zone of *P. edulis*. Samples were collected using a steel root auger (10 cm diameter × 20 cm height). Each 10 cm soil layer containing root material was carefully separated using sharp instruments, sorted, labeled, and transported to the Soil Laboratory at the Hunan Academy of Forestry. Roots were manually separated from soil and washed using spring water over a 600 µm mesh. Root samples were identified by species based on characteristics such as odor, morphology, and color (Finér et al. 1997). Roots were then classified into fine roots (≤ 2 mm) and thick roots (> 2 mm) using vernier calipers (An et al. 2017). All root samples were oven-dried at 60 °C to constant weight before weighing.

The root attenuation coefficient (β) was calculated based on root biomass density across soil depths. Here, Y represents the cumulative percentage of root biomass from the surface to a given depth d (cm). The β value reflects the vertical distribution tendency of roots: lower values indicate shallow root concentration, while higher values suggest deeper root penetration. Importantly, β is not correlated with total root volume or density, but rather characterizes root distribution relative to soil depth. Nonlinear

regression modeling was performed using SPSS 21.0 (IBM, Armonk, NY, USA). To enable comparison across sampling methods, three morphological indices were standardized: specific root length (SRL), root length density (RLD), and root specific surface area (RSA), for both fine and coarse roots. These indices were calculated using the following parameters: L (root length, cm), V (soil sample volume, cm³), W (root dry mass, g), and S (root surface area, cm²). One-way analysis of variance (ANOVA) was used to assess differences in root biomass and morphological traits among forest types and expansion stages, using SPSS 21.0. In addition, redundancy analysis (RDA) was conducted to examine relationships between soil physicochemical properties and root traits, using Canoco 5.0 (Microcomputer Power, Ithaca, NY, USA) with 499 Monte Carlo permutations.

3. Results

3.1 Comparison of root traits between two species in expanding forest stands

Analysis of root traits revealed that only fine root standing length (FRSL) and fine root length density (FRLD) of *Cl* exhibited significant differences among forest stand types ($P < 0.05$), with both traits being significantly higher in the PCM stand compared to the other two (Table 1). For *Cl*, total root length density (TRLD) and total root surface area (TRSA) displayed an increasing trend followed by a decline as the bamboo expansion progressed, whereas total root biomass (TRB) and thick root standing length (TSRL) followed the opposite pattern. In contrast, fine root traits exhibited reversed trends. The root system of *Pe* demonstrated complex, heterogeneous changes with no significant differences across expansion stages. In general, from the PES to PCM stands, TRB, FRLD, and TRLD of *Pe* increased initially and then declined, while other traits followed inverse patterns. In the mixed forest stands, most *Pe* root traits were higher than those of *Cl*, except for TRLD in CLS and PCM; FRSL and fine root surface area (FRSA) in PCM; FRLD in PCM; and TRB across all stages. These findings suggest distinct root system heterogeneity between the two species during bamboo expansion, with *Pe* fine roots exhibiting clear advantages in both biomass and morphological plasticity.

3.2. Vertical distribution of root biomass and soil physicochemical property

The vertical distribution patterns of root biomass for *Cl* and *Pe* varied significantly with bamboo expansion (Fig. 2). In *Cl*, biomass in the upper soil layers decreased while that in the deeper layers increased from CLS to PCM, with similar biomass values observed at a depth of 50 cm. The proportion

of root biomass in the topsoil (0–20 cm) declined markedly from 49.7% to 0.34%. In contrast, *Pe* root biomass decreased steadily with depth from PES to CPM, predominantly concentrating in the 0–20 cm layer. The topsoil biomass ratio dropped from 76.6% to 45.3% in accordance with the increasing number of expanding individuals. Additionally, the β values of *Cl* and *Pe* showed opposite trends along the bamboo expansion gradient (from PES to CLS), indicating contrasting vertical distribution patterns. Most soil physicochemical parameters decreased significantly with depth ($P < 0.05$), except for soil pH, which increased highly significantly ($P = 0.000$), and bulk density, which also increased significantly ($P < 0.05$). Total phosphorus, water discharge capacity, and moisture content did not differ significantly with depth ($P > 0.05$). These results confirm the vertical heterogeneity of soil physicochemical properties in the study area.

3.3 Functional root distribution traits

Analysis of functional root allocation (Fig. 3), revealed that the fine root ratio of *Cl* consistently ranged from 0.5 to 0.6 across soil layers in the CLS stand. However, in CPM and PCM, fine root ratios increased in upper layers and decreased in deeper layers, following a pattern of initial increase followed by a decrease along the expansion gradient. In the PES stand, the fine root ratio of *Pe* increased with soil depth, while the thick root ratio also rose in deeper layers. These observations suggest that root system allocation in both native and expanding species was influenced by bamboo expansion.

3.4 Vertical distribution of root morphological plasticity

As shown in Fig. 4, *Cl* exhibited heterogeneous changes in RLD across soil depths in response to bamboo expansion. Specifically, RLD decreased in upper layers and increased at deeper depths. Similarly, the FRLD of *Pe* declined with depth, while its TRLD in upper layers decreased significantly due to expansion. In pure *Cl* stands (CLS), SRL showed an increasing trend with depth. However, in mixed and expanding stands, SRL values of *Cl* varied across soil layers. Both TRSL and FSRL increased in the upper layers and decreased in deeper layers, although FRSL showed more complex variation. Conversely, SRL of *Pe* in CPM increased with depth, contrasting with patterns observed in PES and PCM. Radial spread area (RSA) values exhibited similar patterns to SRL. These findings suggest that, compared to *Cl*, *Pe* root systems demonstrated relatively stable phenotypic plasticity

across soil depths during expansion. Notably, the 50–60 cm soil depth represented a transition layer where most root morphological traits exhibited pronounced changes, likely due to variations in soil properties.

3.5 Influence of soil environment factors affects to the root traits

As indicated in [Table 2](#), soil environmental factors explained a cumulative variance of 78.07% for *Cl* root biomass traits on Axis 2 and 88.48% for *Pe*. For morphological traits, soil variables accounted for 67.00% and 53.87% of the variation in *Cl* and *Pe*, respectively. These results indicate that soil factors had a stronger influence on *Pe* biomass traits and *Cl* morphological traits. As illustrated by [Fig. 5](#), *Cl* biomass traits (TRB and thick-to-fine root biomass ratio, TFBR) and TRLD were positively correlated with soil pH. Meanwhile, FRSA, FRSL, and TSRL were strongly associated with available nitrogen (AN) and total vegetation frequency (TVF), which in turn affected TFBR, TRSA, and FRLD. In contrast, *Pe* traits were negatively influenced by organic matter (OM) and AN, with RLD, TFBR, FRSL, and fine root elongation surface area (FESA) being more sensitive to AN than to OM. AN also had a strong effect on TRSA and TSRL. A positive correlation was observed between OM and AN. These findings demonstrate that *Cl* and *Pe* differ in their root trait responses to soil environmental factors, reflecting species-specific adaptive strategies.

4. Discussion

4.1 Root biomass distribution and resource acquisition

Root biomass density serves as a direct indicator of a plant's resource acquisition capacity ([Jackson et al. 2000](#); [Wijesinghe et al. 2001](#); [Lynch and Wojciechowski 2015](#)). In this study, the root biomass of Chinese fir showed a significant decline along the vertical soil profile as bamboo expansion progressed from CLS to PCM, accompanied by a reduction in available nutrient content. Although the root biomass of bamboo exhibited a similar vertical trend, the change was not statistically significant, and bamboo roots remained primarily concentrated in the upper soil layers ([Fig. 2](#)). These observations suggest that both native and expanding species may adopt a spatially balanced strategy to minimize direct competition for belowground resources. This balance likely results from spatial heterogeneity and niche differentiation, driven by the vertical distribution of rhizome systems ([McKane et al. 2002](#); [Shen et al. 2016](#)), and is consistent with findings on other types of plant competition ([Yao et al. 2017](#);

Xu J et al. 2019). Bamboo possesses a robust rhizome-root system that efficiently exploits nutrient- and water-rich upper soil layers. Through functional root adjustments, such as increased biomass density and other morphological strategies, bamboo maximizes its resource acquisition efficiency, contributing to the depletion of local resources and ultimately increasing mortality among native species (Ouyang et al. 2016; Wang et al. 2012). Moreover, bamboo expansion alters the structure of soil microbial communities and nutrient mineralization processes, leading to the survival of only a few fine roots in the upper layers where bamboo rhizomes dominate (Li et al. 2017). As soil depth increases, the physicochemical environment becomes more limiting, intensifying intraspecific competition and resulting in the decline of disadvantaged Chinese fir individuals.

This study also revealed that bamboo expansion modified the distribution of the TFBR for both species, as shown in Fig. 3. The proportion of fine roots increased in upper layers but declined in deeper layers, mirroring the vertical trends observed in Fig. 2. Notably, Chinese fir exhibited a limited presence of fine roots in the upper soil, whereas moso bamboo significantly increased its fine root proportion in these layers. These findings suggest that increases in root biomass in deeper soil were largely due to enhanced thick root biomass. As bamboo encroached into Chinese fir stands, the proportion of thick roots increased despite an overall reduction in total biomass. This shift facilitated deeper soil exploration by boosting the thick root system, thereby improving nutrient access. Interspecific resource competition significantly influenced the biomass density and functional allocation of roots. In general, moso bamboo allocated a higher proportion of root biomass to fine roots, providing a clear advantage in nutrient acquisition (Song et al. 2011; Wang et al. 2013). According to the root efficiency hypothesis (Eroot), clonal plants allocate biomass proportionally in nutrient-rich patches but adjust allocation according to resource distribution in poorer environments (Hutchings and John 2003). The asymmetric competition between expanding bamboo and native Chinese fir affected the root-to-shoot ratio (Yao et al. 2017). Additionally, this study excluded roots with diameters greater than 18 mm, as the main taproot systems were primarily located below the rock layer (beyond 80 cm depth). Table 1 indicated that root biomass for both species initially declined and then increased with advancing bamboo expansion, suggesting a stress response to expansion for both native and expanding species. This pattern does not fully support the conclusion by Farooq et al. (2019), who reported a strong correlation between root biomass and plant density—mainly observed in pure plantations dominated by intraspecific competition. In our study plots, nutrient availability decreased with soil depth, and the

subsoil exhibited a high gravel content, which exacerbated the negative impacts of bamboo expansion (Withington et al. 2006). Overall, the results highlight that the rhizome-root system of bamboo had more pronounced advantages in biomass density and vertical distribution stability compared to Chinese fir.

4.2 Response of root phenotypic plasticity to bamboo expansion

New root formation enables plants to adapt to novel environments and respond to soil nutrient heterogeneity through optimized proliferation and efficient resource acquisition (Fitter et al. 1991; Ma et al. 2018). Key morphological parameters—SRL, RLD, and RSA—serve as critical indicators of root phenotypic plasticity, being directly linked to the efficiency of water and nutrient uptake (Kramer-Walter et al. 2016; Zhang et al. 2020). As shown in Table 1, moso bamboo demonstrated superior phenotypic plasticity overall when compared to Chinese fir, aligning with prior findings (Hishi et al. 2015; Cai et al. 2019; Liao et al. 2019). This enhanced plasticity likely confers a competitive advantage in resource acquisition. Across expansion stages, Chinese fir exhibited variable RLD across soil layers, while bamboo maintained relatively stable vertical patterns. These differences can be attributed to shifts in vertical root distribution driven by expansion effects (Withington et al. 2006; Ostonen et al. 2007). In pure forest stands, both species displayed increasing SRL and RSA with soil depth. However, comparative analysis of mixed stands (CPM and PCM) revealed significant interspecific differences in phenotypic plasticity indices (Fig. 4). Chinese fir exhibited declines, while bamboo displayed substantial increases. These trends likely reflect the uneven distribution of soil nutrients, moisture, and lithology, driving divergent morphological adaptations in root systems.

Bamboo's high degree of physiological integration enables effective translocation of resources along source-sink gradients (Ke et al. 2008), providing a marked advantage in nutrient-deficient subsoils. The expanding bamboo population is largely composed of young, physiologically active rhizomes, further supporting its adaptability and survival. The morphological plasticity of the bamboo rhizome system reflects dynamic responses to microenvironmental changes associated with both soil depth and expansion progression. Additionally, an asymmetry exists between the plasticity of fine and thick roots, suggesting distinct functional roles. Root architectural modifications are mainly regulated by endogenous hormones (Kutz et al. 2002), particularly through processes involving meristematic cell elongation and differentiation. Cytokinins, primarily synthesized in root tissues, negatively regulate

root development (Werner et al. 2001, 2003). For example, enhanced cytokinin synthesis suppresses primordia initiation and affects lateral root spacing (Chang et al. 2015), contributing to complex root system architecture. Cytokinin levels are closely linked to plant responses to external environmental variation. While hormone signaling is widely recognized in root development, the specific regulatory mechanisms by which bamboo expansion influences hormone pathways remain poorly understood and warrant further investigation.

4.3 Influence of the soil environment on root growth and distribution

The development and spatial distribution of root systems are predominantly shaped by belowground environmental conditions. In this study, soil factors exhibited a greater influence on root biomass than on morphological traits (Table 2), explaining 78.07% and 88.48% of biomass variation in *Cl* and *Pe*, respectively, while only accounting for 67.00% and 53.87% of variation in morphological traits. This suggests that factors beyond soil physicochemical properties—such as multicollinearity, soil fauna activity, and interspecific root interactions—also play important roles in shaping phenotypic plasticity. Significant differences were also observed in the primary soil drivers affecting root plasticity between the two species. In Chinese fir, phenotypic traits were positively influenced by available nitrogen and pH, whereas in bamboo, traits were negatively correlated with AN and organic matter. These differences are likely attributable to the physical vertical separation of soil layers caused by bamboo expansion. As bamboo spreads, Chinese fir roots are increasingly displaced into deeper subsoil layers characterized by reduced AN and elevated pH, thus exacerbating physiological stress and limiting nutrient uptake (Fig. 2).

Conversely, bamboo rhizome systems remain predominantly concentrated in the nutrient-rich topsoil and exhibit rapid turnover and replacement of senescent roots, thereby maintaining high efficiency in resource acquisition (Eissenstat et al. 2000). Moreover, bamboo expansion modifies native soil physicochemical conditions by increasing fine root biomass and accelerating nutrient cycling, contributing to greater soil heterogeneity. Soil pH plays a critical role in shaping microbial community composition and enzyme activity (Lin et al. 2014), Mitsutoshi et al. (2015) suggested that changes in soil acidity could be linked to bamboo-induced alterations in exchangeable calcium ion concentrations, which in turn accelerate humification of organic matter, enhance ammonification, and suppress nitrification and mineralization processes (Song et al. 2016). These transformations ultimately favor

bamboo proliferation (Zhang 2023). Thus, bamboo expansion not only modifies the root architecture of native species but also reshapes the entire soil environment in a manner unfavorable to native plant survival. Understanding root growth and spatial structure must therefore consider the combined effects of soil physicochemical parameters, microbial communities, faunal activity, lithology, temperature, and interspecific root interactions.

5. Conclusion

This study elucidates the differences in root spatial structure and phenotypic plasticity between expanding bamboo (*Pe*) and native Chinese fir (*Cl*), and reveals the underlying root-level mechanisms through which bamboo forest expansion reduces plant community biodiversity. The results demonstrate that Chinese fir is at a competitive disadvantage compared to bamboo in terms of both root distribution and plasticity, leading to impaired nutrient acquisition in native species. Therefore, enhancing external nutrient inputs may promote the growth and resilience of native arbor species in bamboo-encroached mixed stands. Simultaneously, mitigating soil nutrient depletion caused by bamboo expansion may require active restoration strategies, such as topsoil reclamation and removal of bamboo rhizomes in the vicinity of trees.

Declaration of competing interest

The authors declare no competing interests.

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Contributions

W. S. developed methodology. Z. J. wrote the original draft manuscript. Z. J., S. S and Y. P. conducted

site investigation and treated samples, S. S and Y. P. analyzed the data. Y M, M. Y. and M. Q. participated the research conceptualization. P. C. wrote the revised manuscript. P. C. acquired funding and provided supervision. All authors have read and approved the article.

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538 Tables

539 Table 1

540 The root traits and accumulative coefficient of *Cl* and *Pe* affected by the bamboo expansion.

Root types	Traits	<i>Cl</i>				<i>Pe</i>	
		CLS	CPM	PCM	PES	CPM	PCM
Thick root	<i>TRB</i> (g·m ⁻³)	4512.6±2149.3	3814.6±1897.2*	2596.1±1594	888.6±427.0	910.2±531.5*	1404.4±456.3
	<i>TSRL</i>	43.51±3.73	39.84±6.89**	37.15±6.02**	50.3±3.91	50.12±5.21**	45.07±3.92**
	<i>TRLD</i>	0.037±0.008	0.043±0.013**	0.031±0.009	0.019±0.005	0.024±0.007**	0.045±0.03
	<i>TRSA</i>	33.98±2.03	35.06±4.74*	31.81±2.68	37.13±1.81	40.3±3.16*	36.45±2.05
Fine root	<i>FRB</i> (g·m ⁻³)	584±105.7	197.7±58.4**	456.7±195.2**	1431.7±533.8	1053.9±502.0**	1428.6±312.2**
	<i>FSRL</i>	264.3±19.74b	289.3±25.37b*	355.1±38.81a*	306.2±30.04	327.4±37.45*	264.0±28.61*
	<i>FRLD</i>	0.05±0.006	0.033±0.007**	0.057±0.011**	0.111±0.027	0.1±0.031**	0.117±0.047**
	<i>FRSA</i>	64.35±2.77b	61.75±3.27b*	74.36±3.75a*	72.67±3.53	89.39±13.47*	59.64±3.02*

541 Letters denote the significant difference of each species in forest stands. * and ** denotes the
 542 significant difference ($P<0.05$) and highly significant difference ($P<0.01$) respectively between *Cl* and
 543 *Pe* in the same mixed-interfaces.

544

545

546 Table 2

547 Statistical results of RDA analysis for biomass and soil environment factors. Biomass indexes
 548 include total biomass (*TB*) and thick-fine root biomass ratio (*TFBR*), morphological indexes
 549 include.

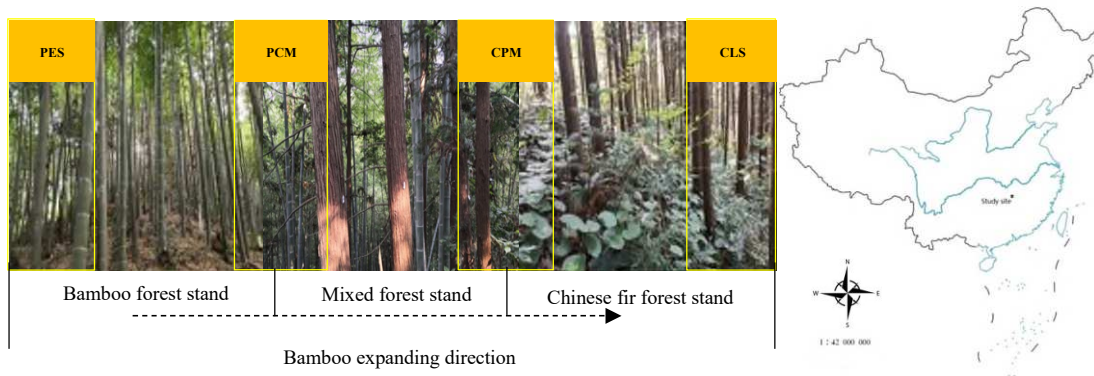
Indexes	Statistic	<i>Cl</i>				<i>Pe</i>			
		Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
Biomass indexes	Eigenvalues	0.629	0.152	0.209	0.010	0.511	0.375	0.090	0.025
	Explained variation (cumulative) (%)	62.85	78.07	98.96	100	51.01	88.48	97.52	100
	Pseudo-canonical correlation	0.878	0.908	0	0	0.9632	0.912	0	0
Morphol-	Eigenvalues	0.406	0.264	0.144	0.067	0.367	0.172	0.155	0.032

ogical	Explained variation								
indexes	(cumulative) (%)	40.6	67	81.43	88.13	36.67	53.87	69.35	72.52
	Pseudo-canonical								
	correlation	0.967	0.997	0.903	0.983	0.943	0.858	0.792	0.671

550

551

552 *Figures*



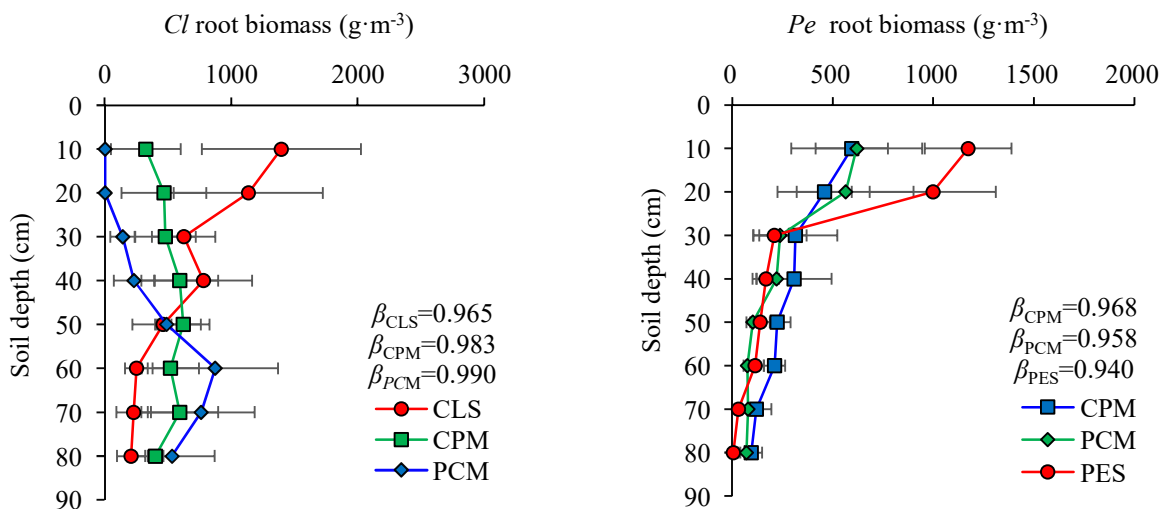
553

554 **Figure 1**

555 **Schematic diagram and location of bamboo expanding belt (width 20 m × length (60±) m with 4**
556 **sub-belts of 20 m × 5 m) in Wannian Forest Farm of middle-southern China, which was divided**
557 **into three forest stands based on species composition along bamboo expanding direction, *l* was**
558 **confirmed according to the bamboo shoots expanding distance.**

559

560



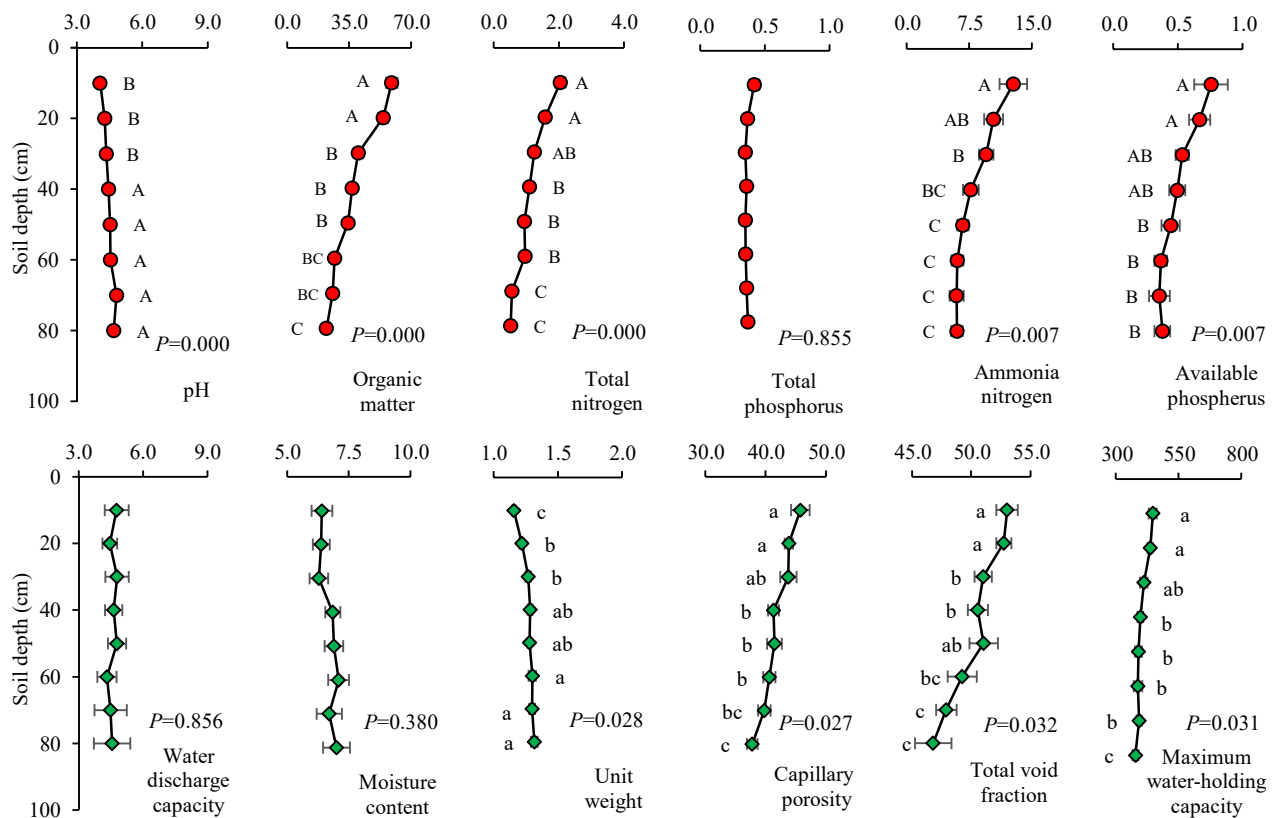


Fig. 2

The vertical distribution of biomasses of *Cl* and *Pe* root (rhizome) system and physicochemical properties of soil by bamboo expansion. One-way ANOVA was conducted to analyze the difference of physicochemical indexes with soil depth.

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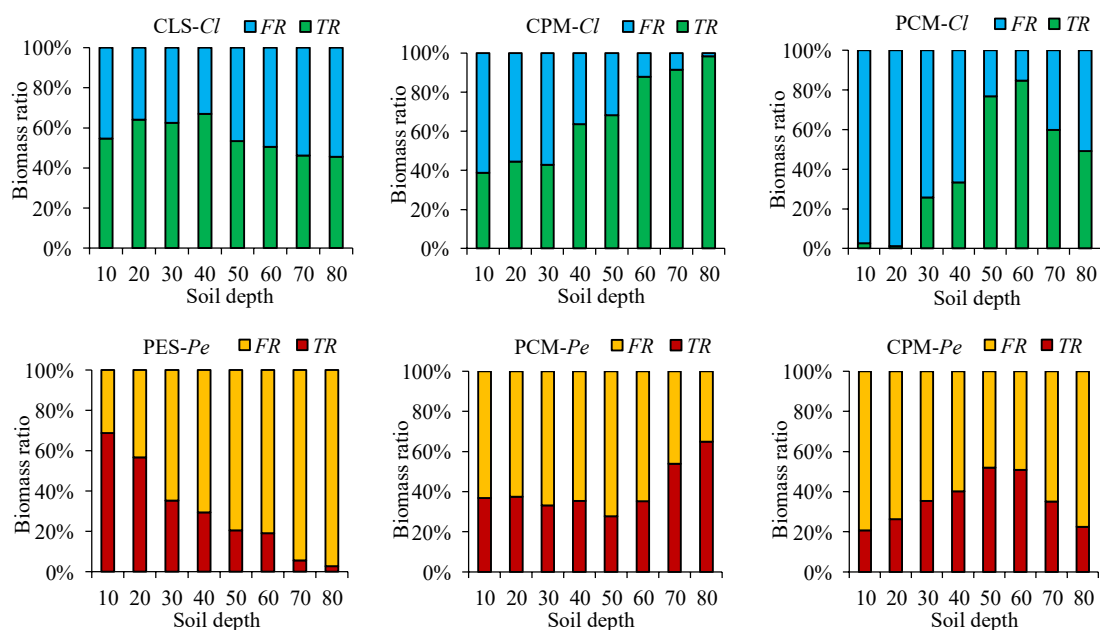
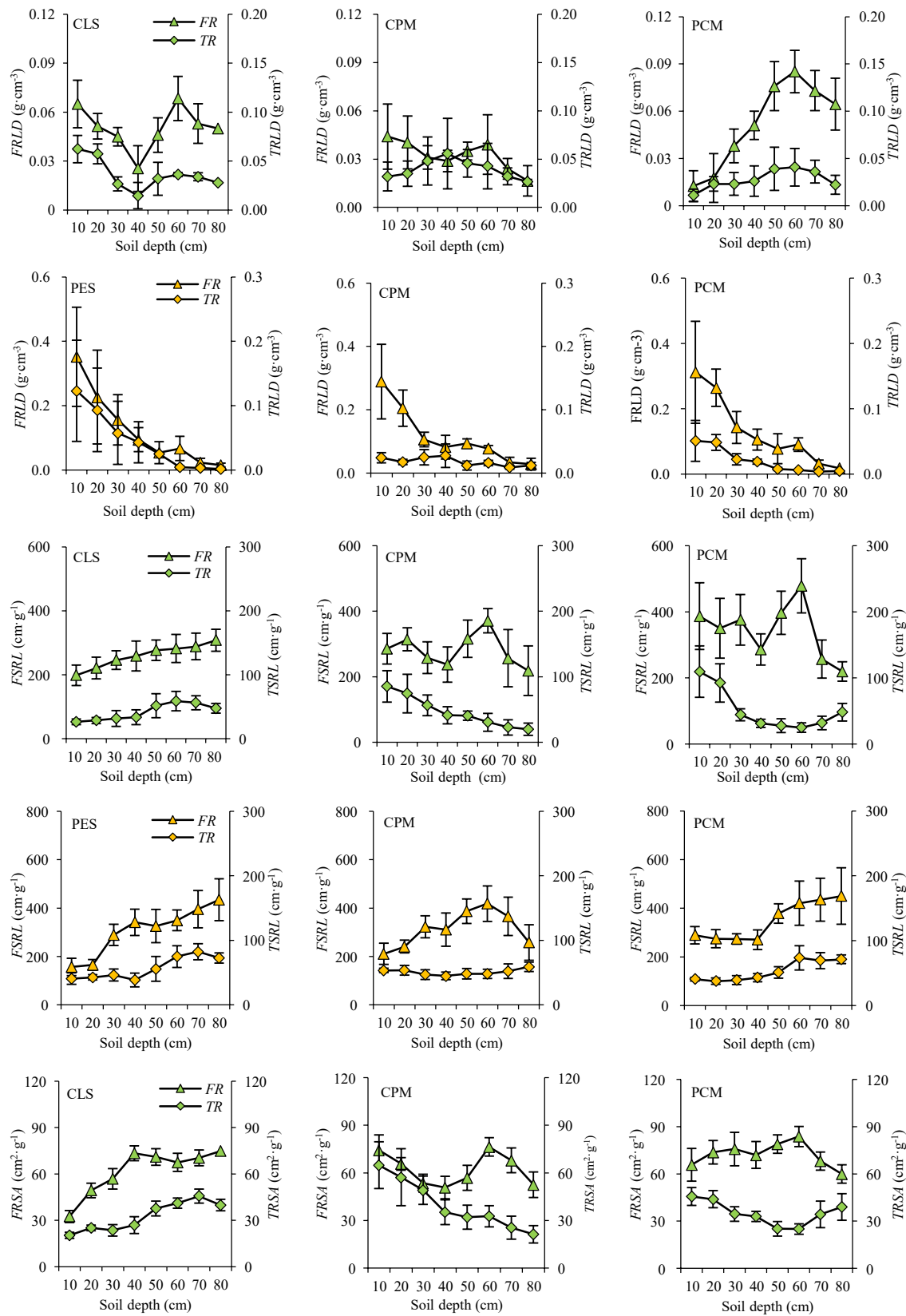


Fig. 3 The biomass ratio between fine root and thick root of *Pe* and *Cl* in the soil layer affected

by the expansion. Therein *TR* is thick root and *FR* is fine root.



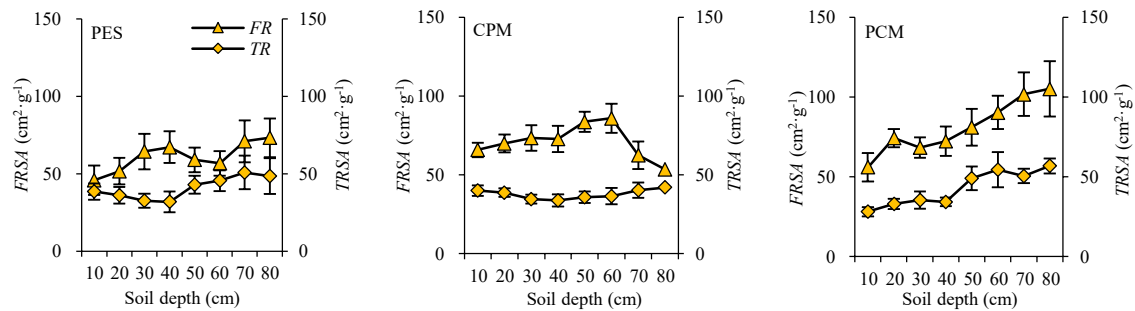


Fig. 4

the morphological traits changing character of *Cl* and *Pe* root systems in soil layers (0-80 cm) with bamboo expansion. The green label was *Cl* and orange label was *Pe*, and the morphological traits were calculated with non-dimensional treatment to eliminate brought about by sampling.

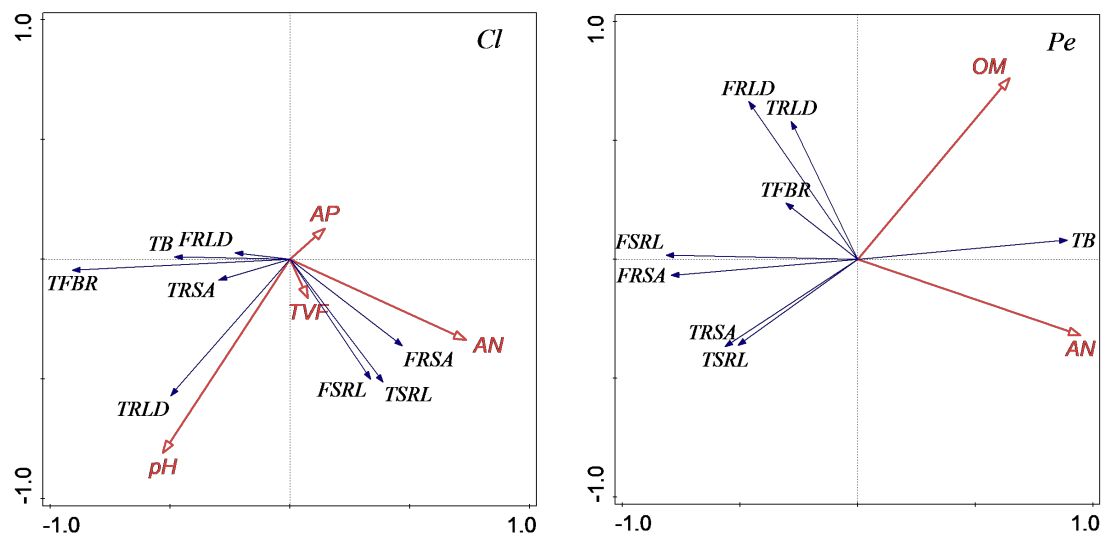


Fig. 5

Two-dimensional redundancy analysis ordinations of *Pe* and *Cl* root trait indexes-soil factors under forward selection. The soil physicochemical indexes *AN*-ammonia nitrogen, *AP*-available phosphorus, *OM*-organic matter, *TVF*-total void fraction, *TFBR*-thick-fine root biomass ratio, *TB*-total biomass.

570

571 Equations

572 $\beta=(1-y)^{\frac{1}{a}}$

573 $SRL=L/W$

574 $RLD=L/V$

575 $RSA=S/W$

576

577

578

579 Abbreviation

580 *Cl* *Cunninghamia lanceolate* (Chinese fir)

581 *Pe* *Phyllostachys edulis* (moso bamboo)

582 PCM mixed stand of moso bamboo with a few Chinese firs

583 CPM mixed stand of Chinese fir with a few moso bamboo shoots

584 CLS pure stand of Chinese fir

585 PES pure stand of moso bamboo

586 *SRL* specific root length

587 *RLD* root length density

588 *RSA* root specific surface area

589

590