

Article

Effects of Different Cultivation Patterns and Bamboo Stand Densities on Growth and Physiological Traits of *Paeonia lactiflora* Intercropped Under *Phyllostachys edulis* Forests

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Abstract

Interplanting *Paeonia lactiflora* Pall. under *Phyllostachys edulis* (Carrière) J. Houzeau (moso bamboo) forests forms an innovative agroforestry intercropping system. This practice has great potential to improve economic benefits and maintain ecosystem stability of moso bamboo forests. Nevertheless, the physiological and growth adaptation mechanisms of *P. lactiflora* in the understory microenvironment of moso bamboo are still poorly understood. In this study, a two-factor field experiment was conducted to examine how moso bamboo stand density (0, 1200, 1800, 2400 plants·ha^{−1}) and cultivation pattern (bag cultivation, field cultivation) shape the growth, root traits, and resource allocation of *P. lactiflora*. The results showed that under bag cultivation, the low bamboo stand density (1200 plants·ha^{−1}) promoted biomass accumulation in *P. lactiflora* leaves, stems, and roots, and facilitated root elongation and radial thickening. Under this condition, *P. lactiflora* adopted a root-prioritized growth strategy and preferentially allocated nitrogen and phosphorus to leaves and roots. For field cultivation, *P. lactiflora* growth was inhibited by dual stresses of aboveground shading and underground interspecific root competition. To cope with such stress, *P. lactiflora* prioritized leaf growth, allocated more nitrogen and phosphorus to leaves, and developed thinner roots. This study reveals the differential growth, root plasticity, and resource allocation strategies of *P. lactiflora* in response to dual stresses of aboveground shading and underground root competition from moso bamboo, filling the research gaps regarding multi-factor adaptation mechanisms of understory herbaceous plants in moso bamboo forests. The optimal undercropping regime combining low moso bamboo stand density with bag cultivation pattern is identified. These findings offer practical references for the efficient and sustainable management of bamboo–peony agroforestry systems and are critical for balancing the economic benefits of moso bamboo stands and maintaining the stability of understory ecosystems.



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Keywords: bamboo stand density; cultivation pattern; *Paeonia lactiflora*; *Phyllostachys edulis*; understory cultivation

1. Introduction

Phyllostachys edulis (Carrière) J. Houzeau (moso bamboo), a monopodial scattered evergreen arborescent bamboo species belonging to the genus *Phyllostachys* of Poaceae, ranks as the bamboo taxon with the broadest distribution and highest economic value across China [1]. Traditional moso bamboo management systems primarily focus on the single

production of bamboo timber and bamboo shoots, resulting in a simplistic industrial structure. In recent decades, persistent declines in the economic profitability of moso bamboo stands have led to widespread abandonment of bamboo forests [2]. Planting commercial crops under moso bamboo can substantially raise the overall economic benefits derived from bamboo stands. This practice also elevates ecosystem biodiversity while improving the soil and water conservation and carbon sequestration functions of bamboo forests [3,4]. *Paeonia lactiflora* Pall. is a perennial rhizomatous herb [5]. Its fleshy tuberous roots contain abundant medicinal constituents including paeoniflorin and albiflorin [6]. As a major traditional Chinese medicinal herb, it possesses outstanding ornamental and medicinal values. The domestic consumption of dried medicinal *P. lactiflora* root in China reached 38,200 tons in 2025, and traditional Chinese medicinal products manufactured from this raw material generated an industrial economic benefit of 6.53 billion CNY. Medicinal *P. lactiflora* roots have been utilized as folk herbal remedies for more than 2000 years. Paeoniflorin in *P. lactiflora* roots exert cardiovasoprotective, neuroprotective and anti-inflammatory effects. These bioactivities have been validated via modern pharmacological assays and standardized clinical prescriptions, rendering *P. lactiflora* roots widely applied in contemporary clinical practice of traditional Chinese medicine. In addition, the commercial value of *P. lactiflora* also covers the sales of cut flowers and seedlings, as well as the production of seed oil. Furthermore, *P. lactiflora* exhibits moderate adaptability to understory habitats [7,8]. Intercropping *P. lactiflora* under moso bamboo forests represents a promising agroforestry model to raise the economic efficiency of moso bamboo forests.

The intensity of interspecific competition among coexisting plants and species adaptability jointly shapes the output and economic gains of underplanted commercial crops [9]. Stand density acts as a critical factor regulating understory microhabitats and the magnitude of interspecific competition [10]. Aboveground, stand density reshapes vertical canopy structure and modulates understory light intensity, temperature, and humidity, thereby triggering morphological and physiological adaptive responses in understory crops [11]. Minor fluctuations in light availability alter leaf pigment concentrations, stomatal conductance, transpiration rates, and photosynthetic efficiency of plants [12,13]. Plants trigger coordinated morphological and physiological plasticity to adapt to variable light gradients, known collectively as the shade avoidance response [14]. Morphological modifications such as taller shoots, longer internodes, larger leaves, and lower leaf mass per area maximize light interception under low illumination [15,16]. For physiological acclimation, plants decrease chlorophyll a/b ratios and regulate internal hormone concentrations [17]. Understory species further alter carbon and nutrient partitioning to alleviate resource limitation caused by shading [18,19]. As illustrated by the carbon gain hypothesis, vegetation reduces nutrient partitioning toward heterotrophic organs (i.e., stems and root systems) while assigning more nutritional resources to foliar tissues for maintaining photosynthetic carbon fixation [20]. Nevertheless, plant shade tolerance varies widely across species, leading to divergent growth strategies and contrasting partitioning patterns of nutrients and photosynthates under fluctuating light conditions [21].

Below ground, stand density and cultivation modes generate root competition of different magnitudes for understory plants [22]. This competitive stress usually inhibits their root growth [23,24]. To alleviate such limitation, understory species reshape root spatial distribution to shrink overlapping resource-foraging regions [25,26]. Plants enhance soil resource acquisition via root morphological plasticity, including elevated root length density, intensified branching, and altered fine-root diameter [27–29]. In terms of resource partitioning, plants allocate more nutrients and photosynthates to lateral roots and root hairs to prioritize root proliferation and strengthen competitive capacity for belowground resources [30]. On the other hand, moderate competition can boost the growth of coex-

isting plants through interspecific allelopathy, nitrogen fixation, and microbe-mediated interactions [31–34]. Clarifying the morphological and physiological adaptive strategies of understory crops to aboveground shade stress and belowground root competition is essential. Nevertheless, most existing research merely focuses on a single environmental stress independently. Few studies have systematically explored the interactive impacts of aboveground shade and underground root competition simultaneously.

Numerous studies have investigated rhizomatous herb intercropping under moso bamboo canopies [35,36]. However, the moso bamboo–*P. lactiflora* agroforestry system represents an innovative cultivation model, and the interspecific interaction mechanisms between the two species remain poorly documented. In this study, we selected *P. lactiflora* cultivated beneath moso bamboo as the research material. A two-factor controlled experiment combining varied cultivation patterns and bamboo stand densities was established to investigate *P. lactiflora* biomass allocation, root morphology, as well as contents of nutrients and non-structural carbohydrates across all treatments. To elucidate the physiological and growth adaptation mechanisms of *P. lactiflora* under different cultivation patterns and bamboo stand densities, three hypotheses were proposed based on our experimental design: (1) cultivation patterns and bamboo stand density jointly regulate the growth of *P. lactiflora*; (2) varied cultivation patterns and bamboo stand densities trigger root morphological plasticity in *P. lactiflora*; (3) under resource limitation driven by shade and underground root competition, *P. lactiflora* prioritizes nutrient allocation to leaves and roots.

2. Materials and Methods

2.1. Experimental Design

The field research plots were established within Moganshan Town, Deqing County, Huzhou City, Zhejiang Province, China (119°87' E, 30°63' N). Moso bamboo stands with consistent stand density, soil texture, soil nutrient status, slope aspect, and gradient were selected for the trial. All moso bamboo individuals within the experimental plots correspond to *P. edulis*, the typical original form devoid of culm morphological aberrations. The soil was yellow soil, with the following baseline physicochemical properties: soil organic matter 45.41 g·kg^{−1}, total nitrogen 2.42 g·kg^{−1}, total phosphorus 0.27 g·kg^{−1}, total potassium 24.6 g·kg^{−1}; alkali-hydrolysable nitrogen 176.4 mg·kg^{−1}, available phosphorus 3.65 mg·kg^{−1}, available potassium 52.3 mg·kg^{−1}; soil pH = 4.78. The peony cultivar used in this study was *Paeonia lactiflora* 'Dahongpao'. The seedlings of *P. lactiflora* used in the experiment were obtained via ramet division from mother plants of a single provenance. The provenance originates from Xinwo Town, Pan'an County, Jinhua City, Zhejiang Province, China. Each ramet seedling retained 12 cm of fleshy roots and two plump buds.

Twenty-four 15 m × 15 m plots were established within the moso bamboo forests. These plots were divided into three separate blocks, each containing eight plots assigned to eight treatments:

- BC-0: Bag cultivation without moso bamboo;
- BC-1: Bag cultivation with moso bamboo stand density of 1200 plants·ha^{−1};
- BC-2: Bag cultivation with moso bamboo stand density of 1800 plants·ha^{−1};
- BC-3: Bag cultivation with moso bamboo stand density of 2400 plants·ha^{−1};
- FC-0: Field cultivation without moso bamboo;
- FC-1: Field cultivation with moso bamboo stand density of 1200 plants·ha^{−1};
- FC-2: Field cultivation with moso bamboo stand density of 1800 plants·ha^{−1};
- FC-3: Field cultivation with moso bamboo stand density of 2400 plants·ha^{−1}.

In November, moso bamboos were harvested and bamboo stumps removed from each plot to achieve the target stand densities. For bag cultivation, *P. lactiflora* were planted in non-woven fabric bags (Guangzhou Fenghe Agricultural Development Co., Ltd., Guangzhou,

Guangdong Province, China) with an inner diameter of 38 cm and a height of 40 cm, filled with topsoil collected from the moso bamboo understory. Seedling fleshy roots were placed vertically into the substrate and covered with a 3 cm layer of soil. After transplanting, all planting bags were evenly arranged on the ground surface of the moso bamboo understory. For field cultivation, *P. lactiflora* seedlings were directly planted into the soil under the moso bamboo canopy. Cylindrical planting pits with uniform specifications (38 cm in diameter and 40 cm in depth) were dug at each planting site prior to transplanting. This practice was implemented to eliminate differences in soil bulk density between bag cultivation and field cultivation. The planting density of *P. lactiflora* was uniformly set at 28,350 plants per hectare across all treatments. The quantitative proportion of one-year-old (1 du), two-to-three-year-old (2 du), and four-to-five-year-old (3 du) moso bamboo is set at an equal ratio of 1:1:1. All moso bamboo aged six years or older were removed. Target stand densities were sustained annually via thinning in November. Manual weeding was conducted twice per year, in June and September, respectively. The schematic diagram of the entire experiment is shown in Figure 1. No additional fertilization or artificial irrigation was applied throughout the cultivation period. No insect pests or pathogenic diseases were observed on *P. lactiflora* during the entire cultivation period. The non-woven fabric cultivation bags used in this trial exhibited excellent drainage and air permeability. Similarly, the field soil for ground-grown peonies possessed favourable drainage capacity, and no waterlogging was observed in the field plots. The experimental cycle lasted for one year. The average temperature in the coldest month (January) was 3.5 °C, and the average temperature in the hottest month (July) reached 28.5 °C. The total precipitation during the experiment was 1379 mm. The temperature variation throughout the experimental period followed the local regular annual pattern, and no extreme weather occurred to interfere with plant growth.

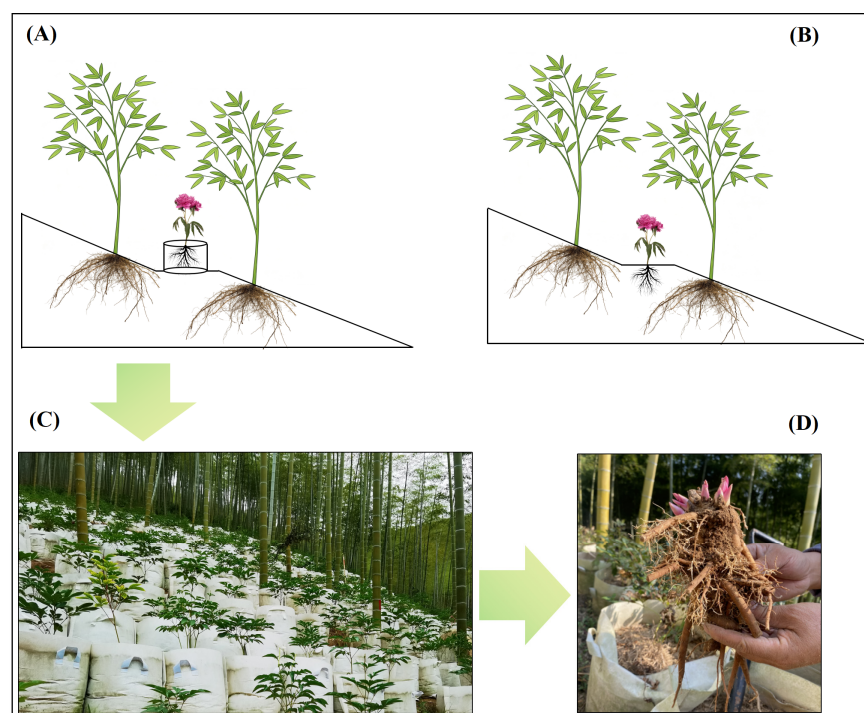


Figure 1. Schematic drawing of the experiment. (A): bag cultivation, (B): field cultivation, (C): photographs of the bag cultivation, (D): root of *Paeonia lactiflora*.

2.2. Harvest and Measurements

After 18 months of cultivation, *P. lactiflora* were harvested in June. Three individual plants were randomly excavated from each plot for whole-plant sampling. Each plant

was separated into stems, leaves, and roots. A 4 mm mesh sieve was used to recover fine roots scattered in the soil. All samples were placed in ice boxes and transported to the laboratory, then temporarily stored in a refrigerator at 0–2 °C. Root samples were rinsed with clean water and blotted dry. Root images were scanned with a dual-sided scanner (Regent Instruments, Quebec, QC, Canada; WinRhizo Pro root analysis system, 300 dpi resolution). WinRhizo software (version 2.0) was used to quantify root morphological traits, including root length, root surface area, and average root diameter. The software further classified roots into five diameter grades (0–0.5 mm, 0.5–1 mm, 1–1.5 mm, 1.5–2 mm, >2 mm) to calculate root length for each diameter grade. After scanning, all plant organs were oven-dried to measure its corresponding biomass. Specific root length (SRL) was calculated as total root length divided by root dry mass. All biomass and root morphological variables of each plot represented the average values of three plants sampled within the plot. All dried organ samples were fully ground. The nitrogen (N) content of leaves, stems, rhizomes, and roots was determined via the H₂O₂–H₂SO₄ digestion method. Phosphorus (P) content was measured using the vanadium-molybdate yellow colorimetric method [37]. The anthrone colorimetric method was adopted to quantify non-structural carbohydrates (NSC), including soluble sugars (SS) and starch (ST) [38].

2.3. Calculations and Statistics

Statistical analyses for all measured traits were completed in SPSS 20.0 (SPSS Inc., Chicago, IL, USA). A two-way analysis of variance (ANOVA) was performed to assess the main effects and interaction effects of bamboo stand densities and cultivation patterns on the response variables. Prior to analysis of variance (ANOVA), the Shapiro–Wilk test and Levene’s test were separately conducted to check data normality and homogeneity of variances, respectively. One-way ANOVA was run for separate single factors, and Tukey HSD post hoc testing was adopted to quantify significant variations between treatment gradients.

3. Results

3.1. Biomass Accumulation and Allocation

Bamboo stand densities and cultivation patterns both significantly affected leaf, stem, and root biomass, as well as root–shoot ratio. Moreover, significant interaction effects were observed for all pairwise combinations of the four indicators (Table 1).

Table 1. Effects of bamboo stand densities, cultivation patterns, and their interactions on indicators.

Indicators	Bamboo Stand Densities	Cultivation Patterns	Bamboo Stand Densities × Cultivation Patterns
Leaf biomass	32.96 **	357.06 **	19.80 **
Stem biomass	15.39 **	298.68 **	12.726 **
Root biomass	98.50 **	604.02 **	70.82 **
Root–shoot ratio	50.80 **	89.97 **	10.83 **
Root length	29.86 **	138.87 **	3.74 *
Root surface area	89.75 **	605.82 **	41.16 *
Root average diameter	18.36 **	265.88 **	19.68 **
Specific root length	24.71 **	215.73 **	18.32 **
Leaf N	38.64 **	55.91 **	0.58
Stem N	34.45 **	1.28	0.15
Root N	2.26	86.70 **	9.46 *
Leaf P	27.07 **	18.06 **	0.57
Stem P	4.80 *	0.65	0.59
Root P	1.80	50.24 **	8.91 **
Leaf ST	5.28 *	53.77 **	0.97
Stem ST	5.84 **	33.00 **	1.09
Root ST	17.66 **	49.83 **	1.43
Leaf SS	27.98 **	17.56 **	0.24
Stem SS	9.29 **	15.12 **	0.42
Root SS	8.71 **	3.42	0.85

Note: the values are F-values; *, $p < 0.05$; **, $p < 0.01$; N: nitrogen, P: phosphorus, ST: starch, SS: soluble sugar.

Biomass of roots, stems, leaves, and root-to-shoot ratio exhibited analogous variation trends. Under the bag cultivation mode, all four indices first increased and then decreased with rising bamboo stand density, peaking under treatment BC-1 and reaching the minimum under BC-3. For field cultivation, the four indices declined continuously as bamboo stand density increased. At an identical stand density, all four indices were significantly higher under bag cultivation than under field cultivation ($p < 0.05$) (Figure 2).

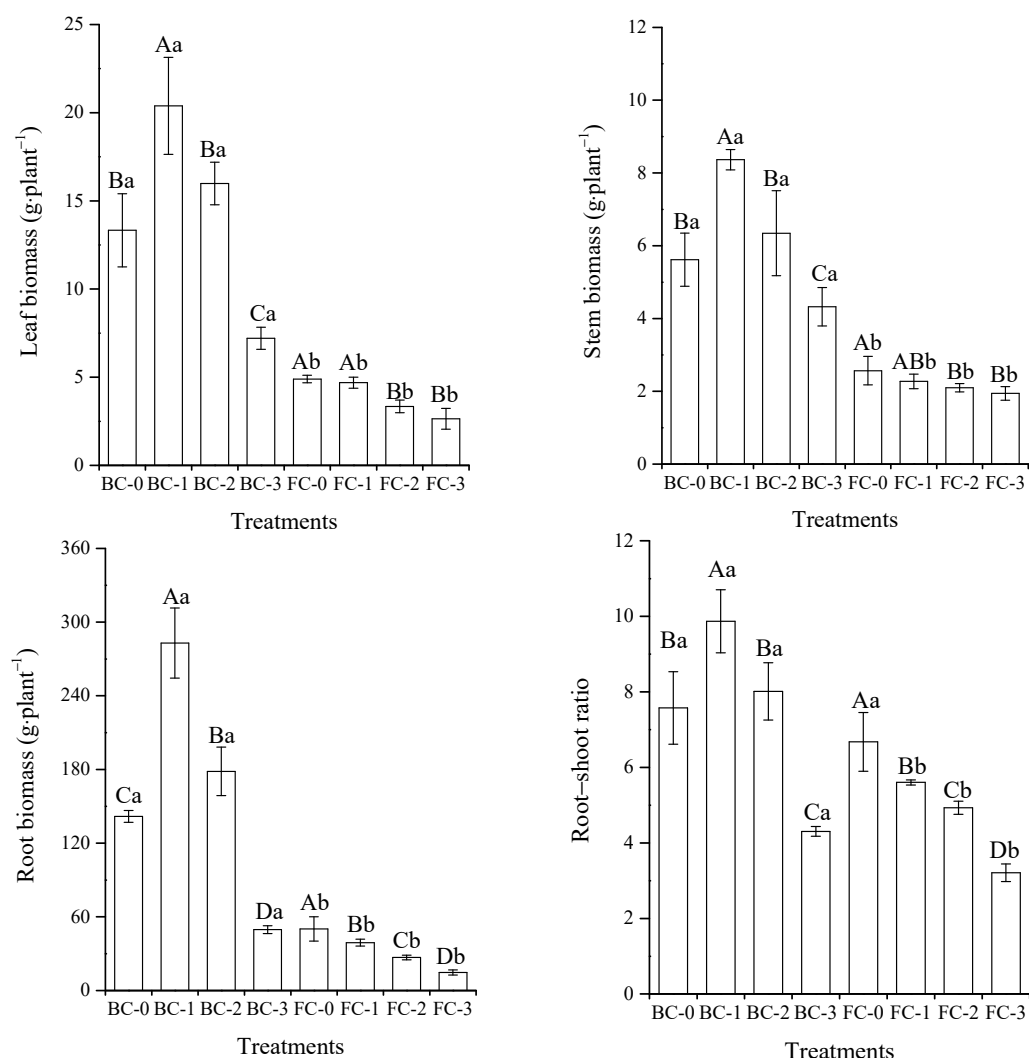


Figure 2. Biomass allocation of *Paeonia lactiflora* under different treatments. Distinct lowercase letters denote statistically significant disparities between cultivation patterns, and distinct uppercase letters denote statistically significant disparities between bamboo stand densities ($p < 0.05$).

3.2. Root Growth and Morphological Characteristics

Bamboo stand densities and cultivation patterns both significantly affected root length, root surface area, root average diameter, and specific root length. Moreover, significant interaction effects were observed for all pairwise combinations of the four indicators (Table 1).

Under bag cultivation, root length, root surface area, and average root diameter all increased first and then declined with rising moso bamboo stand density, with maximum values observed under treatment BC-1. In contrast, specific root length initially decreased and subsequently increased, reaching its minimum at BC-1. For field cultivation, root length under FC-1 was significantly higher than that under FC-0, yet root length gradually decreased as moso bamboo stand density increased. Root surface area in FC-2 and FC-3

was significantly lower than that in FC-0 and FC-1. Compared with FC-0, FC-1, FC-2, and FC-3 significantly reduced average root diameter and elevated specific root length. Root length, root surface area, and average root diameter were greater under bag cultivation than under field cultivation, while specific root length showed the opposite pattern ($p < 0.05$) (Figure 3).

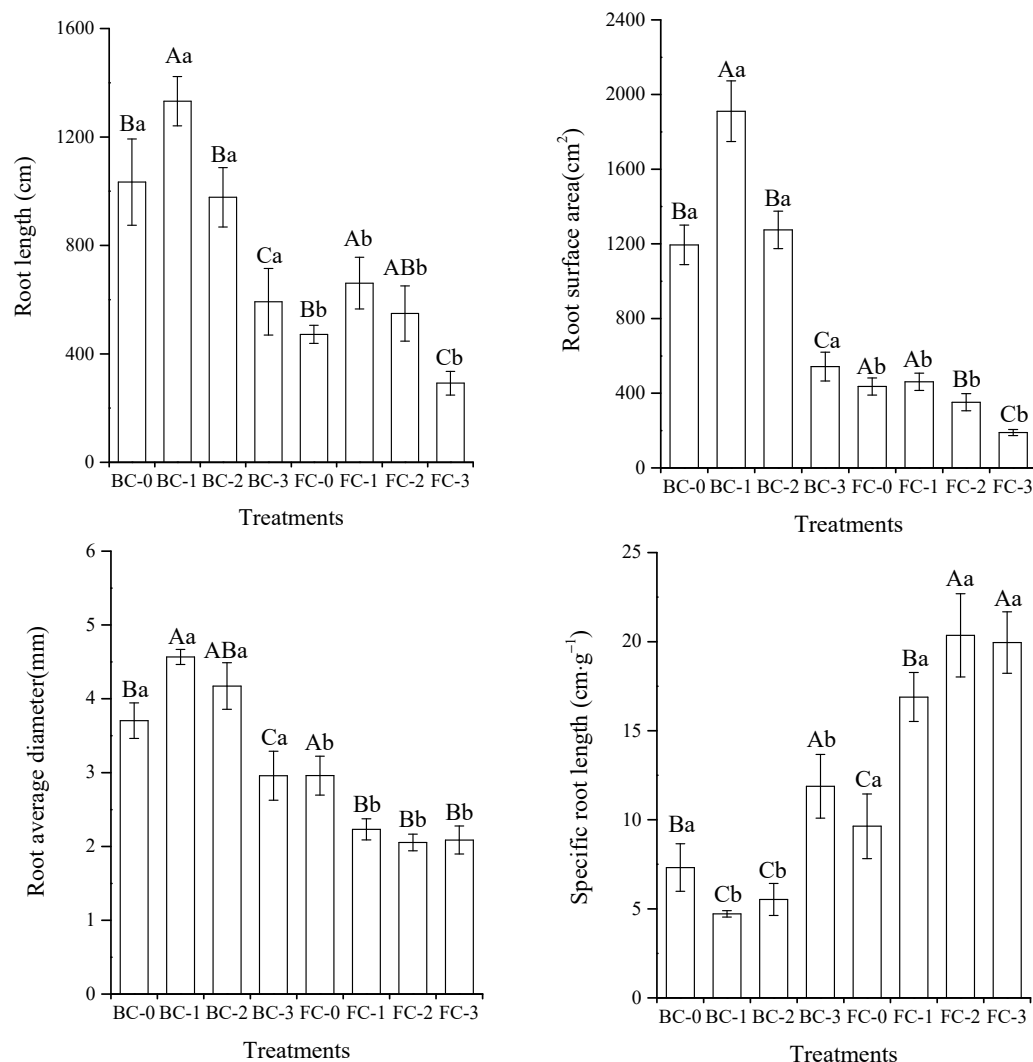


Figure 3. Root morphology of *Paeonia lactiflora* under different treatments. Distinct lowercase letters denote statistically significant disparities between cultivation patterns, and distinct uppercase letters denote statistically significant disparities between bamboo stand densities ($p < 0.05$).

Under bag cultivation, the root length ratio in the 0–0.5 mm diameter grade under BC-1 was significantly lower than that of all other treatments, while its root length and root length ratio in the >2 mm diameter grade were significantly higher. Under BC-3, root length ratio in the >2 mm diameter grade was significantly lower than that under all other treatments ($p < 0.05$) (Figure 4).

Under field cultivation, as bamboo stand density increased, root length of the 0–0.5 mm diameter grade first rose then fell, and its root length ratio increased continuously. By contrast, both root length and root length ratio in >2 mm diameter grade declined gradually. Except for the treatment without moso bamboo, compared with bag cultivation, field cultivation yielded a higher root length ratio in 0–0.5 mm diameter grade and a lower root length ratio in >2 mm diameter grade ($p < 0.05$) (Figure 4).

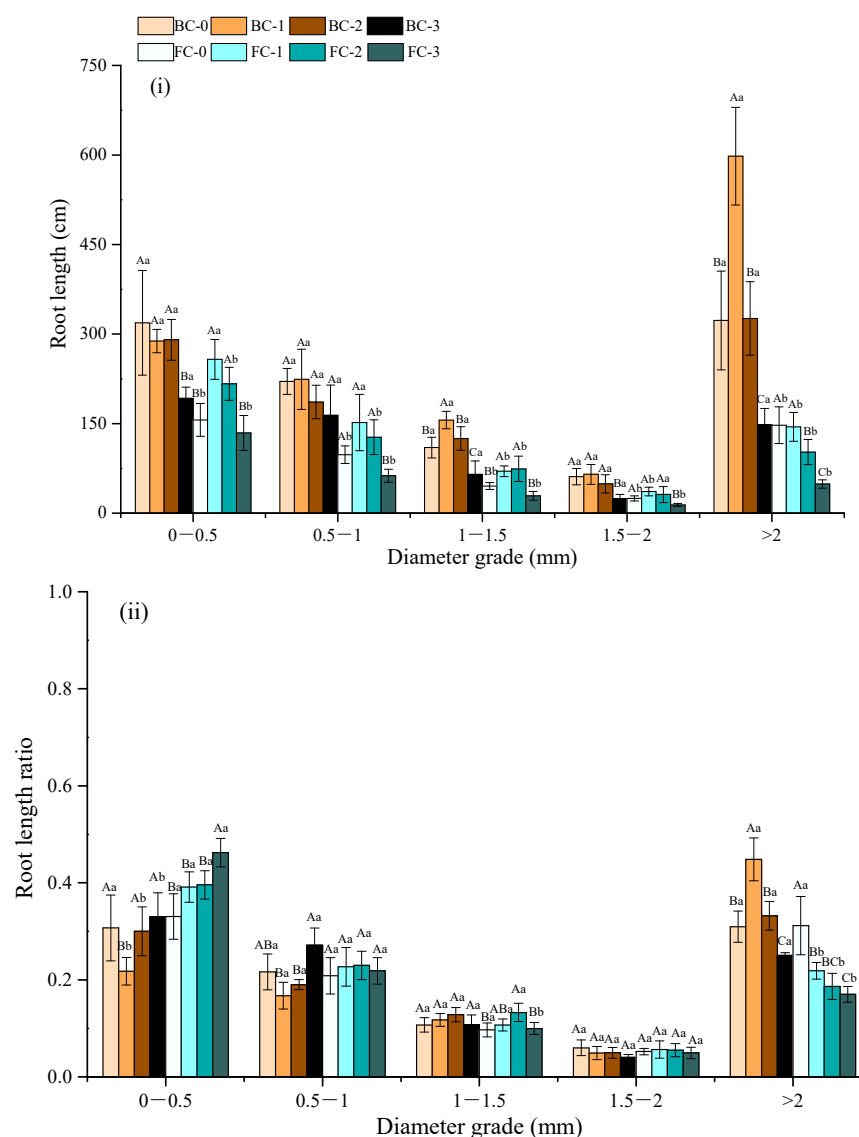


Figure 4. Root length and length ratio across diameter grades under different treatments. Distinct lowercase letters denote statistically significant disparities between cultivation patterns, and distinct uppercase letters denote statistically significant disparities between bamboo stand densities ($p < 0.05$). (i): root length; (ii): root length ratio.

3.3. Nitrogen and Phosphorus Allocation

Bamboo stand density significantly affected leaf N, stem N, leaf P, and stem P. Cultivation pattern exerted significant influences on leaf N, root N, leaf P, and root P. Significant interactive effects between the two factors were detected for both root N and root P (Table 1).

Under bag cultivation, N contents in leaves and roots increased with rising bamboo stand density. Under field cultivation, leaf N content first increased and then decreased as bamboo stand density rose. In contrast, root N content decreased gradually, and this decline was only significant at the maximum stand density (2400 plants·ha^{−1}). Leaf and root N contents under field cultivation were lower than those under bag cultivation, with significant differences observed at higher stand densities (1800 plants·ha^{−1} and 2400 plants·ha^{−1}) (Table 2).

Table 2. Effects of different treatments on nitrogen contents.

Treatments	Nitrogen Contents (mg·g ⁻¹)		
	Leaf	Stem	Root
BC-0	12.64 ± 0.94Ba	9.59 ± 0.69Aa	8.07 ± 0.74Ca
BC-1	13.91 ± 1.03ABa	9.64 ± 0.70Aa	9.62 ± 0.36Ba
BC-2	14.32 ± 0.48Aa	8.57 ± 0.60Aa	9.91 ± 0.29ABa
BC-3	14.94 ± 0.43Aa	8.54 ± 0.45Aa	10.76 ± 1.12Aa
FC-0	11.05 ± 0.70Ba	9.24 ± 0.93Aa	7.63 ± 0.51Aa
FC-1	12.91 ± 0.58Aa	9.53 ± 0.36Aa	7.13 ± 0.60ABb
FC-2	11.57 ± 0.53Bb	8.44 ± 0.51Aa	7.08 ± 0.47ABb
FC-3	11.14 ± 0.31Bb	8.03 ± 0.26Aa	6.63 ± 0.44Bb

Note: Distinct lowercase letters denote statistically significant disparities between cultivation patterns, and distinct uppercase letters denote statistically significant disparities between bamboo stand densities ($p < 0.05$).

Under bag cultivation, P contents in leaves and stems increased first and then decreased with rising bamboo stand density, peaking under treatment BC-1. Root P content under BC-0 was significantly lower than that under the other three treatments. Under field cultivation, leaf P contents exhibited an initial increase followed by a decrease as stand density increased, whereas P contents in stems and roots declined continuously. At bamboo stand densities of 1800 and 2400 plants·ha⁻¹, P contents in leaves, stems and roots were significantly lower under field cultivation than under bag cultivation (Table 3).

Table 3. Effects of different treatments on phosphorus contents.

Treatments	Phosphorus Contents (mg·g ⁻¹)		
	Leaf	Stem	Root
BC-0	2.14 ± 0.13Ba	1.47 ± 0.09Ba	1.73 ± 0.14Ba
BC-1	2.51 ± 0.18Aa	1.71 ± 0.16Aa	2.04 ± 0.20Aa
BC-2	2.42 ± 0.14ABa	1.62 ± 0.07ABa	2.08 ± 0.13Aa
BC-3	2.34 ± 0.10ABa	1.55 ± 0.05ABa	2.09 ± 0.08Aa
FC-0	2.02 ± 0.14Ba	1.56 ± 0.11Aa	1.77 ± 0.10Aa
FC-1	2.36 ± 0.09Aa	1.49 ± 0.03ABb	1.70 ± 0.07ABb
FC-2	2.24 ± 0.16ABb	1.42 ± 0.09ABb	1.66 ± 0.08ABb
FC-3	1.97 ± 0.10Bb	1.35 ± 0.08Bb	1.56 ± 0.12Bb

Note: Distinct lowercase letters denote statistically significant disparities between cultivation patterns, and distinct uppercase letters denote statistically significant disparities between bamboo stand densities ($p < 0.05$).

3.4. Non-Structural Carbohydrate Allocation

Bamboo stand density significantly affected Leaf ST, Stem ST, Root ST, Leaf SS, Stem SS, and Root SS. Cultivation pattern exerted significant influences on Leaf ST, Stem ST, Root ST, Leaf SS, and Stem SS. None of the above indicators exhibited significant interactive effects between the two factors (Table 1).

Under both bag and field cultivation, starch contents in leaves and stems at the highest bamboo stand densities (BC-3 and FC-3) were significantly lower than those under other density treatments. Root starch contents first increased and then decreased with rising stand density under both bag and field cultivation, reaching maximum values at a bamboo stand density of 1200 plants·ha⁻¹ (Table 4).

Under both bag and field cultivation, soluble sugar contents in leaves and stems decreased steadily with increasing bamboo stand density. For bag cultivation, root soluble sugar content under BC-2 was significantly lower than that under BC-0. For field cultivation, root soluble sugar contents under FC-2 and FC-3 were significantly lower than those under FC-0 and FC-1. Cultivation mode exerted minor effects on soluble sugar contents (Table 5).

Table 4. Effects of different treatments on starch contents.

Treatments	Starch Contents (mg·g ^{−1})		
	Leaf	Stem	Root
BC-0	175.65 ± 12.33Aa	178.44 ± 9.98Aa	420.88 ± 25.92Ba
BC-1	177.30 ± 9.86Aa	176.43 ± 6.04Aa	502.51 ± 37.05Aa
BC-2	173.41 ± 12.25Aa	171.64 ± 19.20ABa	486.05 ± 23.49Aa
BC-3	151.28 ± 10.40Ba	146.69 ± 14.33Ba	367.58 ± 38.26Ba
FC-0	148.71 ± 8.79Ab	149.81 ± 8.96Ab	348.70 ± 16.19BCb
FC-1	141.44 ± 5.77ABb	144.13 ± 7.25ABb	396.10 ± 28.34Ab
FC-2	139.90 ± 8.72ABb	145.70 ± 4.91Ab	386.25 ± 30.57ABb
FC-3	132.68 ± 6.51Bb	134.87 ± 4.30Ba	321.15 ± 17.10Ca

Note: Distinct lowercase letters denote statistically significant disparities between cultivation patterns, and distinct uppercase letters denote statistically significant disparities between bamboo stand densities ($p < 0.05$).

Table 5. Effects of different treatments on soluble sugar contents.

Treatments	Soluble Sugar Contents (mg·g ^{−1})		
	Leaf	Stem	Root
BC-0	72.81 ± 3.47Aa	64.73 ± 7.21Aa	92.96 ± 3.26Aa
BC-1	62.07 ± 3.51Ba	56.49 ± 3.64ABa	85.85 ± 9.75ABa
BC-2	61.04 ± 2.24Ba	52.32 ± 2.41Ba	75.61 ± 4.69Ba
BC-3	55.57 ± 3.90Ca	52.61 ± 3.60Ba	80.86 ± 10.86ABa
FC-0	66.10 ± 2.19Ab	56.11 ± 4.84Aa	98.04 ± 7.07Aa
FC-1	58.04 ± 3.17Ba	49.62 ± 2.89ABa	94.58 ± 5.26Aa
FC-2	54.85 ± 4.27BCb	48.63 ± 1.45Ba	83.61 ± 3.01Ba
FC-3	50.93 ± 1.34Ca	46.91 ± 2.18Ba	78.81 ± 3.22Ba

Note: Distinct lowercase letters denote statistically significant disparities between cultivation patterns, and distinct uppercase letters denote statistically significant disparities between bamboo stand densities ($p < 0.05$).

All key results of this study are summarized in Table 6.

Table 6. Overview of key results.

Indicators	Effects of Different Bamboo Stand Densities	Effects of Different Cultivation Patterns	Key Conclusions
Biomass	For root, stem, and leaf biomass as well as the root-to-shoot ratio, comparison with BC-0, BC-1↑, BC-3↓. For stem and leaf biomass, comparison with FC-0, FC-2↓, BC-3↓. For root and root-to-shoot ratio, comparison with FC-0, FC-1↓, FC-2↓, FC-3↓.	BC > FC	Under bag cultivation conditions, shading under low bamboo stand density (1200 plants·ha ^{−1}) benefits the growth of <i>P. lactiflora</i> and promotes biomass allocation to roots. High moso bamboo stand density (2400 plants·ha ^{−1}) significantly reduced the root yield of <i>P. lactiflora</i> by 65.1%.
Root morphological traits	RL Comparison with BC-0, BC-1↑, BC-3↓. Comparison with FC-0, FC-1↑, FC-3↓.	For RL and RD, BC > FC. For SRL, BC < FC.	Under bag cultivation conditions, low bamboo stand densities (1200 plants·ha ^{−1}) facilitated root growth and thickening. Root development and diameter increment were constrained under field cultivation.
	RD Comparison with BC-0, BC-1↑, BC-3↓. Comparison with FC-0, FC-1↓, FC-2↓, FC-3↓.		
	RLR For RLR of 0–0.5mm, Comparison with BC-0, BC-1↑. For RLR of >2mm, Comparison with FC-0, FC-1↓, FC-2↓, FC-3↓. Comparison with BC-0, BC-1↑.		
	SRL Comparison with BC-0, BC-1↓, BC-2↓, BC-3↑. Comparison with FC-0, FC-1↑, FC-2↑, FC-3↑.		

Table 6. Cont.

Indicators		Effects of Different Bamboo Stand Densities	Effects of Different Cultivation Patterns	Key Conclusions
Nutrient element content	N	For root and leaf N, comparison with BC-0, BC-2↑, BC-3↑. For leaf N, comparison with FC-0, FC-1↑, FC-3↓. For root N, comparison with FC-0, FC-3↓.	For N and P in root and leaf, BC-2 > FC-2, BC-3 > FC-3.	In the absence of underground root competition (bag cultivation), <i>P. lactiflora</i> preferentially allocates N and P to leaves and roots to adapt to aboveground shading. When subjected to dual stresses of shading and underground resource competition simultaneously, the <i>P. lactiflora</i> distributes N and P to leaves as a priority.
	P	For leaf, stem, and root P, comparison with BC-0, BC-1↑, BC-2↑, BC-3↑. Comparison with FC-0, FC-3↓.		
NSC content	ST	For ST content in root, comparison with BC-0, BC-1↑, BC-2↑. For ST content in root, stem, and leaf, comparison with BC-0, BC-3↑. For ST content in root, comparison with FC-0, FC-1↑. For ST content in root, stem, and leaf, Comparison with FC-0, FC-3↑.	For ST contents in leaf, stem, and root, BC > FC. For SS contents in leaf, BC > FC.	Low bamboo stand densities promoted starch accumulation in roots, whereas high bamboo stand densities intensified the consumption of both ST and SS.
	SS	For SS content in leaf, Comparison with BC-0, BC-1↓, BC-2↓, BC-3↓. Comparison with FC-0, FC-1↓, FC-2↓, FC-3↓. For SS content in root, Comparison with BC-0, BC-2↓, BC-3↓. Comparison with FC-0, FC-2↓, FC-3↓.		

Note: ↑: increase significantly ($p < 0.05$), ↓: decrease significantly ($p < 0.05$), N: nitrogen, P: phosphorus. RL: root length, RD: root average diameter, RLR: root length ratio, SRL: specific root length, ST: starch, SS: soluble sugar.

4. Discussion

4.1. Biomass Allocation Strategies

The key findings of this study on plant growth are that shade provided under low bamboo stand density (1200 plants ha⁻¹) promotes the growth of *P. lactiflora*. However, biomass decreased linearly with increasing shading intensity. Excessive shading under high bamboo stand density (2400 plants ha⁻¹) drastically reduced peony biomass, which would severely impair its economic yield. Comparisons of biomass between two cultivation patterns reveal that the field cultivation system substantially restricts the growth of *P. lactiflora* due to underground root competition from moso bamboo. The canopy closure under a bamboo stand density of 1200 plants ha⁻¹ ranged from 0.35 to 0.40 [39]. A study on *Indocalamus latifolius* (Keng) under moso bamboo forests similarly confirmed that low bamboo stand densities facilitate plant performance [40]. Previous research reported that the photosynthetic rate of *P. lactiflora* rises with increasing light intensity within a daily cycle [41], yet its light saturation point generally remains below 1300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ [42]. Moderate shading in summer prevents leaf sunburn, elevates ambient humidity and reduces air temperature, thereby favouring *P. lactiflora* growth [43]. It is a widespread observation that appropriate shade promotes plant biomass accumulation [44]. Plants adapt to moderate shade by expanding leaf area and developing thicker, denser leaf tissues [45]. Nevertheless, extreme low-light conditions damage leaf chloroplasts, disrupt photosynthesis and hormone signal transduction, and suppress the outgrowth of leaf buds and new shoots [46]. Accordingly, it can be inferred that full sunlight may impose severe high-light stress on *P. lactiflora*. When bamboo stand density exceeds 2400 plants per hectare, light availability falls below the low-light tolerance threshold of *P. lactiflora*, resulting in photosynthetic inhibition and reduced biomass production.

The key findings of this study on biomass allocation are that when low moso bamboo stand densities boost biomass accumulation in *P. lactiflora*, this species allocates priority to root growth. By contrast, *P. lactiflora* shifts allocation toward leaf growth when its development is suppressed under excessively high bamboo stand densities. Under the combined stress of aboveground shading and underground root competition, peony consistently adopts a leaf-prioritized allocation strategy to sustain carbon assimilation. The biomass allocation strategies adopted by understory crops under low light facilitate efficient light capture, reduce mortality risk, and strengthen their competitive capacity within plant communities [18,47]. Research on *Helianthus tuberosus* L. has demonstrated that moderate shade can elevate root-to-shoot ratio [48]. Existing studies have demonstrated that root competition from neighbouring plants constrains water and nutrient uptake, thereby weakening plant tolerance to low light [49]. Studies on *P. lactiflora* and *Glycine max* (L.) Merr. have observed increased plant height and decreased root–shoot ratios under shade, as plants allocate more resources to stems and leaves [50,51].

4.2. Root Morphological Plasticity

The key findings of this study on root growth are that moderate shading promotes root elongation and radial thickening in *P. lactiflora* in the absence of underground competitive pressure from moso bamboo. Such alterations in root biomass and morphology can effectively improve the economic yield of *P. lactiflora*. Under moderate shading, *P. lactiflora* roots become thicker, whereas the ratio of coarse roots declines under extreme shading. This reflects the carbon allocation strategy of *P. lactiflora* in response to fluctuations in carbon assimilation capacity induced by varying light regimes. When carbon supply is abundant, *P. lactiflora* reduces carbon investment in low-cost, short-lived, absorptive fine roots and prioritizes the development of larger-diameter, longer-lived, storage-type coarse roots to enhance carbon storage capacity. Previous studies have verified that moderate shading facilitates root growth [52,53], yet few investigations have focused on corresponding root morphological traits. Other studies have drawn contrary conclusions, reporting that insufficient light restrains root development, which is generally linked to limited carbon assimilation in aboveground tissues [54]. Under carbon-limited conditions, plants cut investment in high-cost coarse roots and produce more low-cost fine roots to improve nutrient uptake efficiency and sustain basic growth and metabolism [55].

Field cultivation suppresses *P. lactiflora* root growth even under low bamboo stand density. When subjected to underground competition from moso bamboo, *P. lactiflora* produces more fine roots while lowering the ratio of coarse roots. On one hand, moso bamboo roots impose competitive pressure on *P. lactiflora* by occupying soil space and seizing water and nutrient resources. On the other hand, root exudates released by moso bamboo may generate allelopathic substances that inhibit *P. lactiflora* root development [56,57]. Furthermore, the preferential uptake of ammonium nitrogen by moso bamboo may disrupt soil nutrient balance and further restrain *P. lactiflora* root growth [58]. Existing research confirms that interspecific root competition significantly reduces root length density of plants, and the inhibitory effect intensifies with decreasing interplant distance [9]. The strategy of decreasing root diameter to lower total root construction costs to cope with interspecific root competition has been widely documented in prior studies [40,59]. Fine root proliferation largely determines the competitive superiority of coexisting species in nitrogen acquisition [60].

4.3. Nutrient and Photosynthate Allocation

The key findings of this study on nutrient allocation are that under shading, *P. lactiflora* preferentially allocates nitrogen and phosphorus to roots and leaves to boost the growth of

these organs. Under the combined stress of aboveground shading and underground root competition, nutrient concentrations in rhizomes of *P. lactiflora* decrease significantly, while leaf nitrogen and phosphorus contents increase. This indicates that *P. lactiflora* prioritizes nitrogen and phosphorus allocation to leaves when the total nutrient availability is limited. Sufficient carbon supply under moderate shading drives *P. lactiflora* to store carbohydrates as starch in roots, accompanied by the consumption of soluble sugars within root tissues. Previous research on tea reported directional nutrient translocation that stimulates leaf and lateral root development as an adaptation to closed understory canopies [39]. Higher root nutrient contents may also be associated with a greater proportion of fine roots under heavy canopy closure. Fine roots possess much higher nutrient concentrations and stronger nutrient uptake capacity than coarse roots [61]. A study on *Vachellia drepanolobium* (Harms ex Y.Sjöstedt) P.J.H.Hurter found that shaded saplings allocate more carbon to underground storage and accumulate higher starch concentrations in roots. By contrast, saplings grown under full sunlight invest more carbon resources into aboveground growth [62]. Intense root competition from moso bamboo under field cultivation drastically reduces leaf non-structural carbohydrate concentrations, which may be attributed to competition-induced declines in leaf nitrogen and phosphorus levels.

5. Conclusions

In this study, both cultivation pattern and moso bamboo stand density exerted significant main and interactive effects on the growth of *P. lactiflora*. Low moso bamboo stand density facilitates *P. lactiflora* growth and root thickening, whereas high bamboo stand density suppresses *P. lactiflora* development. Under low stand bamboo density, *P. lactiflora* adopted a root-prioritized growth strategy by preferentially allocating nitrogen and phosphorus to leaves and roots to sustain photosynthesis and nutrient uptake. Subjected to underground root competition from moso bamboo, field cultivation drastically restrains *P. lactiflora* growth. Faced with dual stresses of heavy shading and underground resource competition, *P. lactiflora* adapted to adverse environments via developing low-cost fine root systems and switching to a leaf-preferential nutrient allocation strategy.

This study reveals the differential growth, root plasticity, and resource allocation strategies of *P. lactiflora* in response to dual stresses of aboveground shading and underground root competition from moso bamboo, filling the research gaps regarding multi-factor adaptation mechanisms of understory herbaceous plants in moso bamboo forests. This research verifies the feasibility of interplanting *P. lactiflora* under moso bamboo forests and identifies the combination of low moso bamboo stand density and bag cultivation as the optimal intercropping configuration, which can effectively alleviate belowground competitive stress and improve economic yield of *P. lactiflora*. These findings provide practical references for the efficient and sustainable management of moso bamboo–*P. lactiflora* agroforestry systems and are critical for balancing moso bamboo economic benefits and maintaining understory ecosystem stability.

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