EFFECTS OF FOREST CANOPY ENVIRONMENT ON MORPHOLOGICAL PLASTICITY AND PHYSIOLOGICAL RESPONSE OF ARROW BAMBOO (*PSEUDOSASA JAPONICA*) IN COASTAL SANDY AREAS, CHINA

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Abstract. Arrow bamboo (*Pseudosasa japonica*), planted in the state-owned protective coastal sandy forest of horsetail tree (*Casuarina equisetifolia*) in Chishan, Dongshan, Fujian Province, China, was investigated to analyze the morphological characteristics of aboveground components and root systems. The study also examined biomass accumulation, non-structural carbohydrates, antioxidant enzymes, and malondialdehyde levels in arrow bamboo leaves under three forest canopy conditions: large gaps, medium gaps, and forest understory. The results show that each forest canopy environment led to significant differences ($P < 0.05$) in specific morphological characteristics of arrow bamboo, including plant height, basal diameter, under-branch height, total root length, surface area, and volume. Leaf and branch biomass of arrow bamboo in the forest understory was significantly higher than in large- and medium-gap environments ($P < 0.05$). Conversely, culm, stem, root biomass, and total biomass were significantly greater in the large-gap compared to the medium-gap and understory environments ($P < 0.05$). Soluble sugar and starch levels in arrow bamboo leaves were significantly higher in the forest understory compared to the large- and medium-gap environments ($P < 0.05$). Superoxide dismutase, peroxidase, and catalase activities in arrow bamboo leaves were significantly higher in the medium-gap compared to the large-gap ($P < 0.05$). Conversely, the malondialdehyde concentration in arrow bamboo leaves exhibited an opposite trend. It was conclusion that the leaf physiological responses of arrow bamboo. enhances its adaptability to coastal sandy land by modulating morphological characteristics, biomass allocation, and regulating leaf antioxidant enzyme activity.
Keywords: *coastal sandy land, arrow bamboo, leaf, canopy environment, resilience*

Introduction

Morphological plasticity, as defined by Ming (1996), encompasses adaptive alterations in plant morphology within heterogeneous habitats, serving as a mechanism for organisms to acclimate to environmental fluctuations. The common morphological plasticity indexes of plants include plant height, basal diameter, under-branch height, total root length, total root surface area, total root volume and biomass. Furthermore, plants exhibit adaptive modifications in their physiological functions in response to varying light intensities within heterogeneous habitats, optimizing the utilization of available light energy and augmenting their adaptability to the environment (Beneragama et al., 2011; Johnson et al., 2005). In particular, osmotic adjustment substances and antioxidant enzymes are often used to reflect the strength of plant stress resistance. In their study, Xie et al. (2023) observed that shade-tolerant tree species decrease their growth rates and accumulate more non-structural carbohydrates (NSCs) in shaded conditions, ensuring enhanced survival chances for seedlings in the face of an imbalanced carbon budget. Photosynthetic organs in plants have evolved diverse protective mechanisms to mitigate potential damage from light intensity. These mechanisms include the removal of reactive oxygen species, such as superoxide radicals ($O^{2-}\cdot$), hydroxyl radicals (·OH), and hydrogen peroxide (H_2O_2), through enzymatic reaction systems like superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD). Indeed, the concentration of antioxidant enzymes (SOD, CAT, POD) and the level of malondialdehyde (MDA) in plant leaves increase up to a certain threshold with the escalation of light intensity (Liu et al., 2012; Zhao et al., 2022). Bamboo plants exhibit relatively high photosynthetic rates, and numerous species are well-suited for understory growth due to their robust phenotypic plasticity in diverse canopy environments. For instance, the leaf area, leaf thickness, and leaf dry matter content of hou bamboo (*Phyllostachys nidularia*) and green bamboo (*Bambusa oldhami*) increased with rising light intensity (Zhang et al., 2021). Additionally, *qinling*arrow bamboo (*Fargesia qinlingensis*) exhibits the largest diameter at breast height under conditions of medium and large forest gaps (Wang et al., 2006). Because physiological indexes such as non-structural carbohydrates, antioxidant enzymes and malondialdehyde content can reflect the intensity of plant response to adversity conditions, it is of great significance to explore the changes of these indexes of bamboo plants under adversity stress.

The forest gap, also known as gap or canopy gap, stands out as a key feature within the canopy environment. The forest gap directly enhances the light influx within its space (Muscolo et al., 2007), subsequently influencing photosynthesis as well as other physiological and metabolic processes in plants, thereby shaping plant regeneration, growth, and development (Wang et al., 2016). Furthermore, the canopy environment exerts an influence on forest spatial structure and plant community composition, serving as a significant driving force for species regeneration and forest succession. In a study by Sha et al. (2023), forest gaps were identified to actively enhance the diversity of vascular plants and facilitate species symbiosis within the spruce (*Picea asperata*) forest in Qinghai. Additionally, alterations in the understory light environment contribute to the enhanced differentiation of bamboo niches in coastal sandy lands (Lin, 2018).

Coastal shelter forests are natural or artificially created forests in coastal areas that resist natural disasters, improve the ecological environment, and protect production. They perform important ecological functions such as windbreaks, sand fixation, water conservation, species diversity maintenance, climate regulation, and soil and water conservation (Zhang, 1993). Most plants are unsuited for growth in the

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southeastern coastal sandy soils of China, which are predominantly sandy wind and tidal soils with high salt levels, poor water retention, and low fertility (Fan et al., 2017). Therefore, adaptation of the introduced plants to coastal soils is critical for developing specific ecological management and production methods (Jing et al., 2018). Bamboo is a clonal plant that exhibits rapid nutritive growth and asexual reproduction. Once planted, they can be used indefinitely (Zhang et al., 2007). Their rhizomes and roots are entangled and coiled, making them ideal for coastal windbreaks and sand fixation. The introduction of different bamboo species has become an effective approach for increasing the diversity of the coastal sand shelterbelt (Lin et al., 2013; Zheng et al., 2021). Arrow bamboo (*Pseudosasa japonica*) is a rhizome-type bamboo species that was introduced into the horsetail tree (*Casuarina equisetifolia*) shelter forest in the coastal sandy lands of Dongshan County in Fujian Province. It has exhibited good adaptability to growth under the forest. Studies have found that arrow bamboo can adapt to the barren environment, prolong the life of leaves to improve the net accumulation of assimilation products of leaves, shorten the compensation time of leaves, reduce the investment of aboveground parts, and strengthen the development of underground parts, so as to improve its adaptability to the habitat of coastal sandy land, and arrow bamboo forest can effectively improve soil quality (Li et al., 2022, 2023). However, not many studies have reported on the morphological plasticity and physiological responses of the arrow bamboo leaves to the canopy environment.

Therefore, this study analyzes arrow bamboo in coastal sandy land and hypothesizes that change in the canopy light environment induces changes in the aboveground component characteristics, root morphological differences, biomass accumulation and distribution characteristics of each component, concentration of leaf non-structural carbohydrates, antioxidant enzymes and malondialdehyde of arrow bamboo. Three canopy environments with large forest gaps, medium forest gaps, and understory were established for this experimental investigation. The results of this study will provide a theoretical and technical basis for promoting the growth of bamboo populations in coastal shelter forests and understanding their adaptive strategies.

Materials and methods

Research site overview

The research was conducted at the Chishan state-owned protective forestry field in Dongshan Island, Fujian Province (117° 24′ 36″ E, 23° 38′ 15″ N), which has a subtropical oceanic monsoon climate and distinct dry and wet seasons. Droughts occur from November–February, and rainfall is primarily concentrated from May–September with a maximum temperature of 36.6 °C, minimum temperature of 3.8 °C, and average annual temperature of 20.8 °C. The average annual rainfall is 1113 mm and the average annual evaporation is 2013 mm. Droughts and typhoons are the most common natural disasters at this site, with typhoons occurring mostly in July and August. The soil is coastal sandy type. Natural vegetation is scarce. The protected coastal forests are primarily composed of tree species with high resistance and adaptability such as horsetail tree and slash pine (*Pinus elliottii*). An experimental forest comprising of arrow bamboo was established in 2001. No artificial cultivation measures have been undertaken since the introduction of this species, and the bamboo forest has grown well.

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Research site setup

To measure the canopy environment of the arrow bamboo experimental forest, the size of the forest gap was taken as the ratio of the gap diameter (*D*) to the average height of the specimen at the edge of the gap (*H*) (Gálhidy et al., 2006; Hu et al., 2010). *D*:*H* = 0.5 is the understory (FU); *D*:*H* = 1.0 is the medium gap (MG); and *D*:*H* = 1.5 is the large gap (LG). *D*:*H* ≥ 2.0 pertains to the forest edge open space and does not belonging to the forest gap (Qi, 2017).

Canopy light conditions were investigated for each gap sample plot. The sky view factor (SVF) of the three canopy environments was obtained using RayMan Pro 3.1 software to analyze the hemispherical image of the forest gap. Then, the edge of forest gap was identified and its gap diameter was measured by processing and analyzing the image. The height of the specimen at the edge of the gap was measured by using altimeter, and the average height was calculated. The light intensity (LI) of each plot was measured using an illuminometer. Leaf area index (LAI) was measured using an LAI-2200 canopy analyzer (Wei et al., 2003). The canopy environments of each plot are presented in *Table 1*.

Three canopy environments, namely, understory, middle forest gap, and large forest gap, were selected in the distribution area of arrow bamboo. Nikon D7000 digital cameras were set up at the north and south edges and at the central position of each forest gap. A fisheye lens was used to obtain the whole-sky view factor of arrow bamboo in different canopy environments in sunny and cloudless weather at 8:30, 10:00, 15:00 and 16:30 h in four basic positions (i.e., east, south, west, north) and central positions of each canopy gap (Lu et al., 2018), and the light intensity of each plot was measured (*Fig. 1*). The average of the values from all three directions was noted as the light intensity of the understory, medium gap, and large gap, which were 60.24, 23.57, and 4.20 klx, respectively. The area of each canopy environment plot was 10 m × 10 m. The experiment was a complete randomized design with 6 replicates, and continuous measurements were taken for 3 days with a total of 54 samples. *Table 1* and *Figure 1* refer to the work of Zhang et al. (2021).

Table 1. *Canopy conditions of arrow bamboo*

Canopy environment	**Canopy index**			
	D:H	**Sky view factor**	**Light intensity/klx**	**Leaf area index**
Large gap	1.69 ± 0.08	0.259 ± 0.03	60.24 ± 13.01	1.358 ± 0.12
Medium gap	1.02 ± 0.12	0.141 ± 0.02	23.57 ± 5.95	2.430 ± 0.31
Understory	0.34 ± 0.15	0.071 ± 0.03	4.20 ± 2.15	3.301 ± 0.22

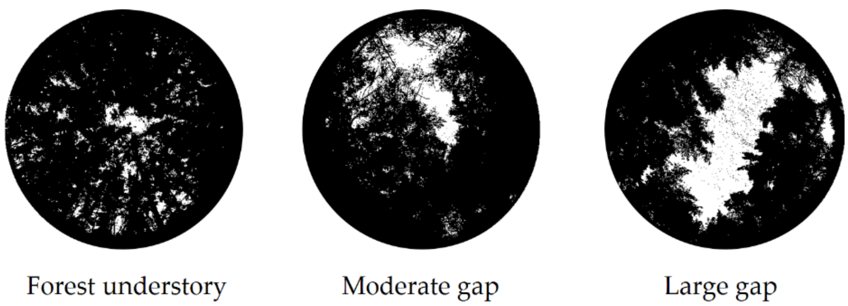

Figure 1. *Hemispherical photograph of canopy gap of arrow bamboo*

Test methods

Determination of morphological indicators of the above-ground components

Three standard bamboo samples were selected from each sample plot by felling. Straightedges and steel tape were used to measure plant height, crown width, under-branch height, and length of the branchlets in the current year. A protractor was used to measure the branching angles of branchlets during the current year. Vernier calipers were used to measure the basal diameters of bamboo stems and branchlets.

Measurement of root morphology indicators

Three small sample squares (1 m × 1 m) were set up in each sample plot. After cutting down the standing bamboo into small sample squares, the complete root systems of the plants were carefully dug up while avoiding root breakage as much as possible. The soil and impurities attached to the root systems were gently shaken off and transported to the laboratory in self-sealing bags. The roots were then rinsed with low-temperature deionized water and dried to remove excess water. The fine roots were scanned using a root scanner, and the total root length, total root surface area, average root diameter, and total root volume were measured using WinRHIZO (version 4.0b, Rengent Instruments Inc., Canada) software.

Determination of the biomass of each component

Three standard bamboo samples were selected from each sample plot by felling. The plants were then dug up with intact root systems and cleaned with deionized water to remove soil and debris from the surface. Next, the excess water was drained. The leaves, branches, stems, roots, and culms of each fresh standard bamboo plant were weighed, and 200 g of each component was placed in a self-sealing bag and transported to the laboratory. The samples were heated in an oven at 105 °C for 30 min before drying at 80 °C for approximately 72 h until the samples reached a constant weight. The dry weight of each component was converted to biomass, and the biomass percentage of each component was calculated.

Determination of non-structural carbohydrates

The dried leaves were ground and passed through a 0.149 mm sieve to determine the levels of non-structural carbohydrates in the leaves, namely, starch and soluble sugars, using anthrone colorimetry.

Determination of antioxidant enzymes and malondialdehyde content

SOD, CAT, POD, and MDA levels were measured using the nitrogen blue tetrazolium, ultraviolet absorption, guaiacol, and thiobarbituric acid methods, respectively.

Data processing

The parameters were calculated using the following formulae: crown spread (m^2) = π × north–south crown length × east–west crown length/4; offset crown index = north–south crown length/east–west crown length; specific root length ($cm \cdot g^{-1}$) = root length/dry weight; root specific surface area ($cm^2 \cdot g^{-1}$) = root surface area/dry weight; and root tissue density ($g \cdot cm^{-3}$) = dry weight/root volume.

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Microsoft Excel 2019 was used for data statistics and processing, and SPSS software was used for one-way analysis of variance (One-way ANOVA). The experimental data were expressed as mean ± standard deviation, and the general linear regression model was used to fit the morphological plasticity and leaf physiological response of arrow bamboo. Origin 2018 software was used for mapping. Canoco 5.0 software was used for redundancy analysis of the correlation between the canopy environment, morphological plasticity, and leaf physiological response of arrow bamboo.

Results

Morphological plasticity of arrow bamboo under different canopy environments

Morphological characteristics of aboveground components of arrow bamboo under different canopy environments

The aboveground components of arrow bamboo exhibited morphological plasticity in different forest canopy environments, with the morphological indicators of plant height, basal diameter, and under-branch height decreasing in the following order of forest gaps: large gaps, medium gaps, and understory. Significant differences were found among all forest canopy environments ($P < 0.05$). Compared with the height of arrow bamboo in large gaps, that of arrow bamboo in the medium gap and understory was reduced by 26.48% and 58.26%, respectively; the basal diameter was reduced by 26.34% and 53.79%, respectively; the under-branch height was reduced by 42.22% and 75.00%, respectively. However, no significant differences ($P > 0.05$) were observed in branchlet length, branchlet diameter, branching angle, crown width, or bias crown index of arrow bamboo in the different forest canopy environments (*Fig. 2*).

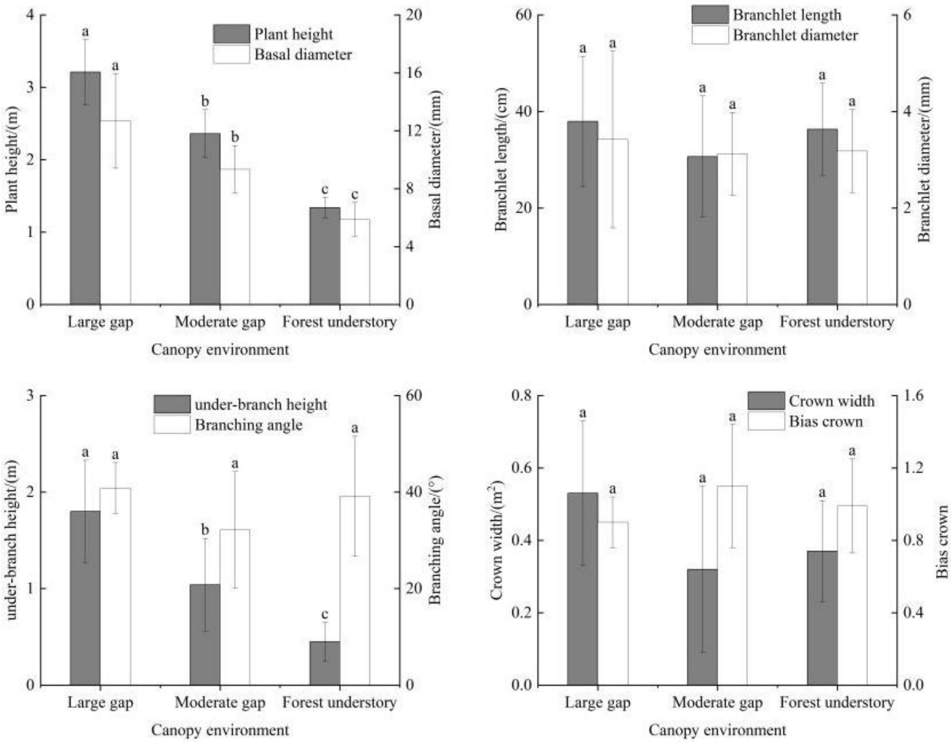

Figure 2. *Differences in morphological characteristics of aboveground components of arrow bamboo under different canopy environments*

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Differences in root morphology of arrow bamboo under different canopy environments

The underground root morphology of arrow bamboo differed in different forest canopy environments. The total root length, surface area, and volume was significantly greater in large gaps than in the medium gaps and the understory ($P < 0.05$). However, no significant differences were observed in underground root morphology between the medium-gap and understory environment. The total root length of arrow bamboo was significantly increased by 24.18% and 32.09% in large gaps compared with that in medium gaps and the understory. The total root surface area increased by 24.91% and 29.39%, respectively, and the total root volume significantly increased by 22.28% and 29.07%, respectively. Other morphological indicators such as mean root diameter, specific root length, specific root surface area, and root tissue density of arrow bamboo did not differ significantly among the different forest canopy environments ($P > 0.05$) (*Fig. 3*).

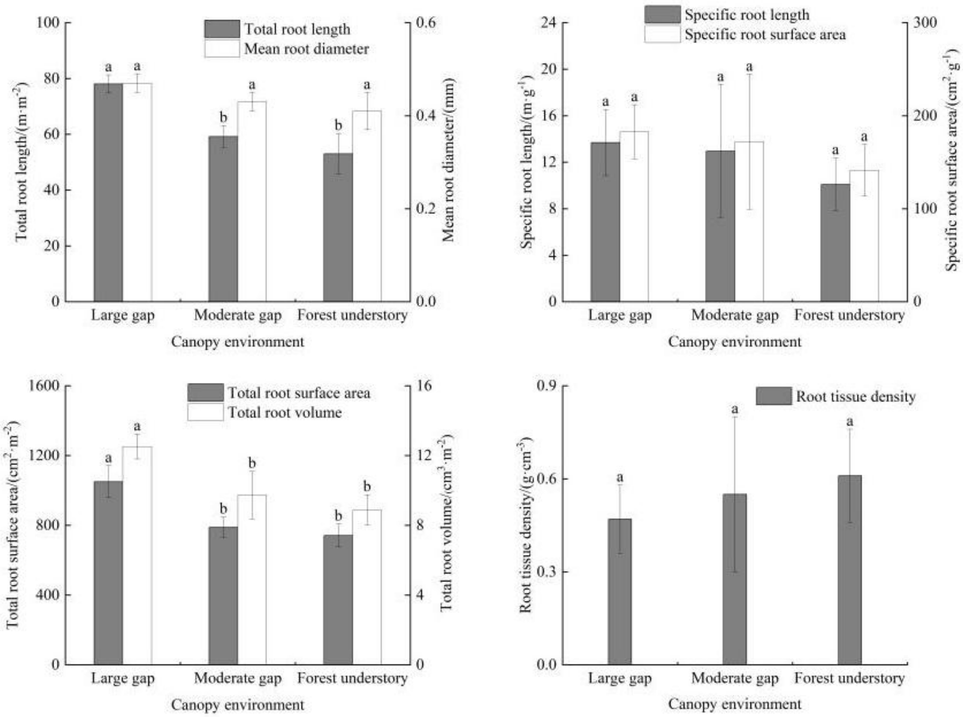

***Figure 3.** Differences in root morphological characteristics of arrow bamboo under different canopy environments*

Biomass accumulation and distribution of each arrow bamboo component under different canopy environments

The biomass and biomass percentage of each arrow bamboo component and total biomass varied significantly depending on the canopy environment. The leaves and branches had the highest biomass in the understory with a high level of canopy closure. This was significantly greater than the amount of biomass of the component in the large and medium gaps ($P < 0.05$). The biomass of stems, roots, and culms decreased in the following order of forest gap: large gaps, medium gaps, and understory; the culm biomass in the large gaps was significantly higher than that in the medium gaps and understory ($P < 0.05$). Stem and root biomass varied significantly among the three

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forest canopy environments ($P < 0.05$). The total biomass of arrow bamboo was significantly greater in the large gaps than in the medium gaps or the understory ($P < 0.05$). Arrow bamboo allocated more biomass to leaf and branch growth and less to stem, root, and culm growth in the understory under low light conditions ($P < 0.05$) (*Figs. 4* and *5*).

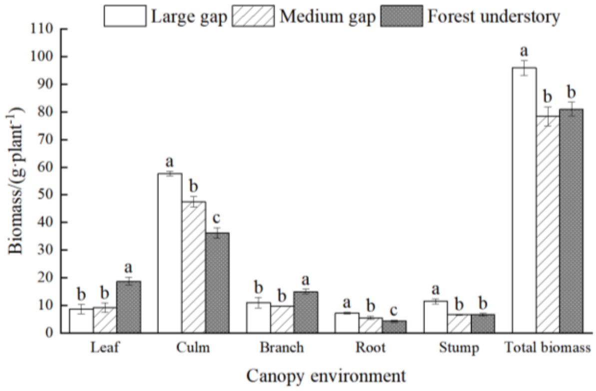

Figure 4. *Differences in organ biomass of arrow bamboo under different canopy conditions*

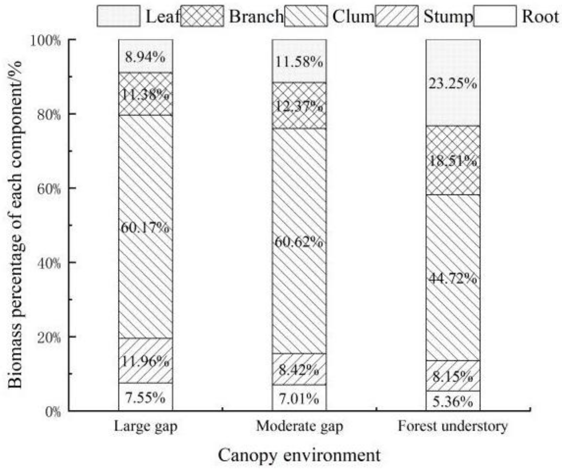

Figure 5. *Differences in biomass distribution among arrow bamboo under different canopy conditions*

Physiological response of arrow bamboo leaves under different canopy environment

Differences in nonstructural carbohydrate content of arrow bamboo leaves under different forest canopy environments

Non-structural carbohydrates (NSC), including soluble sugars and starch, reflect physiological and metabolic activities, the level of carbon supply, and the adaptability of plants to environmental conditions. The soluble sugar and starch content of arrow bamboo leaves varied significantly with the canopy environment. The soluble sugar content in medium gaps and the understory significantly increased by 15.11% and 92.99% ($P > 0.05$), respectively, and the starch content significantly increased by 28.91% and 96.10% ($P > 0.05$), respectively, compared with that in large gaps (*Table 2*).

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Table 2. *Difference in non-structural carbohydrate content of arrow bamboo in different canopy environments*

Canopy environment	Nonstructural carbohydrates	
	Starch/mg·g^{-1}	Soluble sugars/mg·g^{-1}
Large gap	43.38 ± 5.60c	48.50 ± 2.14c
Medium gap	55.92 ± 2.63b	55.83 ± 2.40b
Understory	85.07 ± 3.20a	93.60 ± 4.50a

Difference in antioxidant enzyme activities of arrow bamboo leaves in different forest canopy environments

The activity of all three enzyme were lowest in arrow bamboo plants in large gaps, whereas SOD activity increased significantly by 10.49% and 6.44% in plants in medium gaps compared with those in large gaps and the understory ($P > 0.05$), respectively. POD activity in plants in medium gaps and the understory increased significantly by 9.11% and 9.37%, respectively, compared with those in plants in large gaps ($P > 0.05$). CAT activity in plants in medium gaps and the understory increased significantly by 36.66% and 27.41%, respectively, compared with those of plants in large gaps ($P > 0.05$) (*Table 3*).

Table 3. *Differences in antioxidant enzyme activities of arrow bamboo under different canopy environments*

Canopy environment	Antioxidant enzyme activity of leaves		
	SOD/U·g^{-1}FW	POD/U·g^{-1}FW·min^{-1}	CAT/U·g^{-1}FW·min^{-1}
Large gap	1247.24 ± 42.56b	4242.67 ± 197.64b	96.67 ± 1.04b
Medium gap	1378.05 ± 31.18a	4629.33 ± 72.59a	132.11 ± 6.48a
Understory	1294.72 ± 22.95b	4640.00 ± 123.22a	123.17 ± 5.35a

Difference in malondialdehyde content of arrow bamboo leaves in different forest canopy environments

MDA is a product of lipid peroxidation in plant cell membranes, and its level reflects the degree of damage to the plant cell membrane system. The MDA content in plants in large gaps increased significantly by 53.00% and 43.97%, respectively, compared with those in plants in the medium gaps and the understory (*Table 4*).

Linear regression analysis between morphological plasticity, leaf physiological response and canopy environment of arrow bamboo

In this study, morphological plasticity and physiological indices with significant differences in different canopy environments were selected for linear regression analysis. Plant height, basal diameter, under-branch height, total root length, total root surface area, total root volume, leaf biomass, culm biomass, root biomass, stump biomass, starch, and soluble sugar content in the leaves of arrow bamboo showed highly significant linear correlation with the canopy environment ($P < 0.01$). The branch biomass of arrow bamboo and the POD, CAT, and MDA contents in the arrow bamboo leaves showed a significant linear correlation with the canopy environment ($P < 0.05$).

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However, no linear correlation was observed between SOD content in arrow bamboo and the canopy environment ($P > 0.05$). Culm biomass and SOD content had the highest ($R^2 = 0.978$) and lowest ($R^2 = 0.103$) degree of fit with the canopy environment, respectively (*Table 5*).

Table 4. *Differences in malondialdehyde content of arrow bamboo under different canopy environments*

Canopy environment	Malondialdehyde/μmol·g^{-1}
Large gap	34.41 ± 2.80c
Medium gap	22.49 ± 0.99b
Understory	23.90 ± 0.74b

Table 5. *Linear regression model between morphological plasticity, leaf physiological response, and canopy environment of arrow bamboo*

Dependent variable	Linear regression model	Standardized coefficient	R^2	P
Plant height	Y = 0.438 + 1.863X	0.983	0.966	0.000
Basal diameter	Y = 2.473 + 6.82X	0.927	0.860	0.000
Under-branch height	Y = −25.889 + 135.667X	0.887	0.787	0.001
Total root length	Y = 3749.876 + 3364.217X	0.909	0.827	0.001
Total root surface area	Y = 112.746 + 104.382X	0.892	0.797	0.001
Total root volume	Y = 12.578 + 8.88X	0.810	0.656	0.008
Leaf biomass	Y = 22.396−10.213X	−0.854	0.730	0.003
Culm biomass	Y = 25.684 + 21.467X	0.989	0.978	0.000
Branch biomass	Y = 15.912−4.04X	−0.669	0.448	0.049
Root biomass	Y = 2.802 + 2.887X	0.952	0.906	0.000
Stump biomass	Y = 3.378 + 4.843X	0.847	0.717	0.004
Starch	Y = 103.149−41.69X	−0.958	0.917	0.000
Soluble sugars	Y = 111.079−45.103X	−0.924	0.853	0.000
Superoxide dismutase	Y = 1354.146−47.48X	−0.320	0.103	0.401
Peroxidase	Y = 4901.333−397.333X	−0.745	0.555	0.021
Catalase	Y = 143.816−26.5X	−0.695	0.483	0.038
Malondialdehyde	Y = 16.419 + 10.51X	0.778	0.606	0.013

Correlation analysis between morphological plasticity, leaf physiological response, and canopy environment of arrow bamboo

Redundancy analysis was performed using morphological plasticity and leaf physiological response of arrow bamboo as response variables and the canopy environment as explanatory variables. The results showed that the first ordination axis explained 71.40% of the total spatial variation, the second ordination axis explained 18.13% of the total spatial variation, and the cumulative interpretation explained 89.53% of the total spatial variation. The canopy environment positively correlated with SOD, CAT, POD, starch, soluble sugar content, leaf biomass, and branch biomass. Canopy environment negatively correlated with MDA content, plant height, basal diameter, under-branch height, total root length, total root surface area, total root volume, culm biomass, root biomass, and bamboo biomass (*Fig. 6*).

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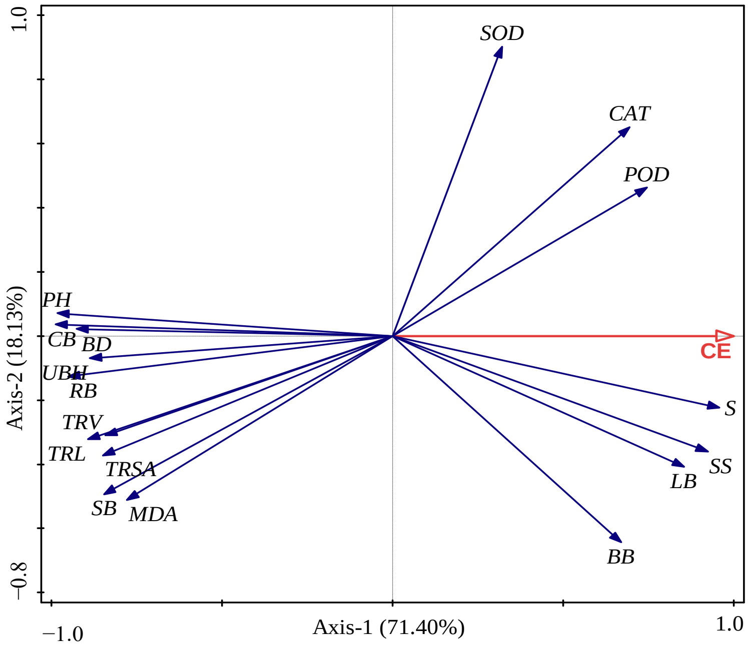

***Figure 6.** Redundancy analysis between morphological plasticity and physiological response of arrow bamboo and canopy environment. CE, canopy environment; PH, plant height; BD, basal diameter; UBH, under-branch height, TRL, total root length; TRSA, total root surface area; TRV, total root volume; LB, leaf biomass; CB, culm biomass; BB, branch biomass; RB, root biomass; SB, stump biomass; S, starch; SS, soluble sugars; SOD, superoxide dismutase; POD, peroxidase; CAT, catalase, and MDA malondialdehyde*

Discussion

Effects of canopy environment on morphological plasticity of arrow bamboo

Light intensity, spectral composition, and other properties of the forest gap and understory regions differ significantly in space and time (Wang et al., 2015). Light is an important ecological factor for plant growth and development (Wang et al., 2010). Under heterogeneous light environments, bamboo plants adapt to habitat changes by regulating leaf functional traits, plant height, basal diameter, crown size, and biomass allocation to promote their growth (Wang et al., 2006; Johnson et al., 2005). The findings of this study showed that the morphological characteristics of arrow bamboo growing in coastal sandy areas display increased plasticity and sensitivity to changes in the canopy environment, as evidenced by the significant reduction in plant height, basal diameter, and under-branch height with decrease in canopy light intensity. These results may be attributed to the low level of photosynthetically active radiation in the low-light habitat of the understory, which limits the accumulation of plant photosynthetic products (total biomass) and restricts plant culm growth, resulting in reduced plant height and basal diameter (Huang et al., 2018). However, increase in light intensity increased plant height, basal diameter, and under-branch height of arrow bamboo to maximum values in large-forest-gap environment.

As the root system is an important plant organ that enables water and nutrient uptake, its growth directly affects overall plant growth, development, and nutrient absorption (Guo et al., 2018). Additionally, the plasticity of root morphology is an important manifestation of the ability of plants to obtain resources such as light, water, and

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nutrients in their living space. The increase in canopy light intensity leads to the loss of soil moisture under the forest, resulting in a shortage of soil water resources (Wu et al., 2023; Li et al., 2023). In contrast, it causes the concentration of organic carbon, nitrogen, phosphorus, and other nutrients in the soil to decrease (Zhang et al., 2021). The findings of this study indicate that the total root length, surface area, and volume of arrow bamboo were significantly higher in large gaps than in medium gaps and the understory. This may be attributed to low soil moisture content of the bamboo forest in coastal sandy land (Liu et al., 2020) and low soil nutrient content in large-forest-gap environment. Therefore, in arid and nutrient-poor soil environments, arrow bamboo increases its total root length, total root surface area, and total root volume to increase the surface area and volume of its roots for increased water absorption, which improves its water and nutrient absorption efficiency and survival adaptation (Keser et al., 2014; Hutchings, 2012). This is a growth strategy used by bamboo plants to actively adapt to changes in the canopy light environment.

Biomass is an important indicator of plant interaction with their environment, and it reflects the ability of the plant to adapt to its surroundings. It also reflects the pattern of plant growth and development (Tang et al., 2015). The plasticity of biomass allocation in clonal plant ramets and ramet components is critical for plants to adapt to heterogeneous habitats and is valuable for understanding the mechanisms underlying ecological adaptations in plants (Ma et al., 2019; Hutchings, 1997). This study found that arrow bamboo captures light energy in the understory environment by modulating the biomass and biomass allocation ratio, which is reduced in the culms, roots, and stumps and increased in the leaves and branches. This facilitates the full use the limited light resources available under the forest canopy to alleviate the impact of adversity. However, no significant difference in the total biomass of arrow bamboo was observed between the understory and middle-forest-gap environments, indicating that arrow bamboo possess strong shade tolerance and is adaptable to low-light environments. In the large-gap environment, reducing leaf biomass allocation and increasing culm biomass allocation may be the phenotypic regulatory behavior for reducing water consumption and increasing water storage (Liang et al., 2017; Wang et al., 2017).

Effects of canopy environment on physiological response of arrow bamboo leaves

NSCs (primarily starch and soluble sugars), which are products of photosynthesis, are the major source of energy required for plant respiration, growth, development, and metabolism. Additionally, they assist plants in resisting habitat stress (Li et al., 2018). In this study, the starch and soluble sugar contents of arrow bamboo leaves significantly increased in the understory low-light environment. arrow bamboo leaves responded to stressful environments by reducing their growth rate and increasing the nonstructural carbohydrate concentration among other adaptive mechanisms in a low-light environment (Poorter et al., 2007). Some studies have shown that low light environment can promote the photosynthetic carbon gain of shade-tolerant plants (Valladares et al., 2008; Poorter et al., 2010). This suggests that arrow bamboo better adapts to understory low-light environments by increasing its nonstructural carbohydrate reserves.

To resist damage from reactive oxygen species, plant cells have evolved to acquire a protective enzymatic system, which primarily includes SOD, CAT, and POD. The primary role of SOD is to promote the disproportionation of superoxide anions and generation of hydrogen peroxide, which is the first line of defense against reactive oxygen species damage in plants (Huo et al., 2022). POD and CAT are responsible for

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the further decomposition and scavenging of hydrogen peroxide in the plant body to reduce damage caused by adversity stress (Jiang et al., 2009). In the present study, the magnitude of SOD and CAT activity in arrow bamboo leaves increased in the following order under different canopy environments: medium gaps > understory > large gaps; the magnitude of POD activity increased in the following order of forest gap: understory > medium gaps > large gaps. This study showed that moderate light intensity in medium-gap habitats was most favorable for the plant in terms of resisting reactive oxygen species and better protecting the cell membrane system, whereas extremely strong or too weak light in large gaps or the understory, respectively, might act as stressor that affect plant growth and damage its resilience (Wang et al., 2023). This indicates that arrow bamboo has a strong shade tolerance and is better adapted to low-light environments. The MDA level is an important basis for judging the degree of membrane lipid peroxidation. The higher the MDA content, the greater the degree of cell damage. In this study, the MDA level in arrow bamboo leaves tended to decrease and then increase with decreasing light intensity in the forest canopy. MDA concentration reduced in the following order based on forest gap: medium gaps < understory < large gaps. In medium-gap habitats, the cell membrane system showed lesser damage than that in all other cases, indicating that moderate light helps alleviate membrane lipid peroxidation.

Relationship between morphological plasticity, leaf physiological response, and canopy environment of arrow bamboo

Plant height, basal diameter, branch height, total root length, total root surface area, total root volume, leaf biomass, branch biomass, culm biomass, root biomass, stump biomass and the concentrations of starch, soluble sugar, POD, CAT, and MDA in arrow bamboo leaves linearly correlated with the canopy environment, which has a significant synergistic or tradeoff relationship with the morphological plasticity and physiological response of arrow bamboo leaves, especially with respect to culm biomass (Huang et al., 2023). The results of redundancy analysis explained 89.53% of the morphological plasticity and physiological response of arrow bamboo under different canopy environments and could better explain the relationship between morphological plasticity and physiological response of arrow bamboo and the canopy environment. The index that was most affected by the canopy environment was culm biomass and the least affected was SOD content. The results show that arrow bamboo improves its adaptability to coastal sandy lands by changing its morphological characteristics, biomass allocation, and regulating the activity of the antioxidant enzymes in its leaves.

Conclusion

In summary, arrow bamboo in coastal sandy areas exhibit morphological plasticity and physiological responses to different canopy environments. In the understory environment, which has great canopy closure and poor light conditions, the growth of individual arrow bamboo plants was stunted because reduced culm growth is necessary for increasing biomass allocation to the branches and leaves to improve the efficiency of light energy capture; additionally, stunted growth helped increase the non-structural carbohydrate reserve in the leaves to meet the growth needs of the plant. In the medium-gap environment with moderate light conditions, arrow bamboo showed reduced MDA levels and enhanced SOD, POD, and CAT activities in the leaves, which slows the

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damage caused by adversity stress. In the large forest-gap environment with a low level of canopy closure and adequate light conditions, arrow bamboo improved its water and nutrient uptake efficiency for survival by increasing the total length, surface area, and volume of its roots. Therefore, arrow bamboo had strong adaptability to difficult site habitats in coastal sandy land. The introduction of arrow bamboo in coastal sandy land could prevent wind and sand, maintain water and soil and protect biodiversity, which played an important role in ecological management and economic production of coastal sandy land.

Author contributions. Yinghui Zhang designed of the research and wrote the manuscript; Xing Cai, Meng Zhang and Dongyong Lai conducted an investigation; Jundong Rong and Liguang Chen gathered and curated taxonomic data; Yushan Zheng were responsible for the administration and supervision of the project; Tianyou He was responsible for funding acquisition. All authors provided comments and suggestions towards the final version of the manuscript, and all authors have read and agreed to the published version of the manuscript.

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