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Forest Canopy Structures and Bamboo Rhizome Internodes Impact the Appearance Quality of Bamboo Shoots

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Abstract: Bamboo shoots are a healthy vegetable with significant commercial value, and their appearance quality is a key factor influencing consumer preference and market pricing. Their growth characteristics—after being unearthed, they maintain basal diameter while rapidly growing in height—affect the taste and nutritional quality. However, little attention has been given to the impact of bamboo forest management on shoot appearance. Therefore, this study addressed this research gap through a comprehensive investigation across three types of bamboo forests: evergreen broad-leaved forest (EBF), evergreen deciduous broad-leaved mixed forest (MBF), and pure bamboo forest (PBF). In addition, we further assessed factors that potentially affect the appearance quality of bamboo shoots, including canopy structures, understory light factors and understory soil factors, mother bamboo factors, and shoot internal factors (pigments and cells). The basal diameters of shoots in PBF and MBF were 1.89 cm and 1.97 cm, respectively, which were significantly larger than those in EBF by 0.27 cm and 0.35 cm, respectively. The linear mixed effect model identified the number of bamboo rhizome internodes and the chlorophyll *a* content as primary factors influencing basal diameter thickening and elongation growth of shoots, respectively. In addition, increasing the bamboo canopy and mean leaf angle reduced the chlorophyll *a* content and increased the carotenoid content, thereby benefiting the improvement in or maintenance of the taste and quality of shoots. This study highlighted that increasing the number of bamboo rhizome internodes, bamboo canopy, and mean leaf angle is helpful to improve the appearance quality of shoots. These findings offer a scientific foundation for bamboo forest management, contributing to both ecological sustainability and economic benefits.

Keywords: bamboo shoots; canopy structure; chlorophyll; forest management; rhizome

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1. Introduction

Bamboo shoots are a vegetable that has important economic value [1]. They are an important resource output of bamboo shoot forests and are one of the main bulk export agricultural products in China, with an annual consumption of more than 2 million tons [1]. The appearance quality of shoots, including fresh mass, basal diameter, and height [2,3], is the primary factor determining consumers' preferences and one of the key factors in market pricing. After the shoots are unearthed, they have the characteristics of rapid growth [4]. While a large amount of nutrients is consumed for shoot cell elongation, the protein (nutritional quality) of shoots decreases [5], and a large amount of cellulose and lignin deposition (taste quality) is required to offset the sudden increase in mechanical pressure during rapid cell growth [6–8], which means that the taste and nutritional quality of shoots decrease [9], thereby reducing their commercial value [10,11]. The morphological development and growth rate of shoots may affect the taste and nutritional quality of shoots.

The basal diameter shows almost no radial growth after shoots emerge from the ground [12]. Bamboo shoots are developed from the internodes of bamboo rhizomes. The nutrients for shoot growth are mainly provided by the connected mature mother bamboo through its underground rhizome [13–15]. Rhizomes store and allocate nutrients by increasing the length and number of rhizome segments [16]. The structure (morphological structure and spatial location) of mother bamboo affects its competitiveness to nutrients [17]. Therefore, the aboveground structure of the mother bamboo and the number and diameter of bamboo rhizomes may have an important influence on the basal diameter of the shoots. The developmental sequence of shoot internodes is basal-oriented, from the basal internode to the top, and the elongation of shoot internodes is determined by the number of shoot cells and cell elongation occurring simultaneously at the elongation stage [5,6,18]. Some studies have shown that the pigment content changes in some early plants' growth, and morphogenesis changes are regulated by the complex regulatory network of lights and hormones [19,20]. Because there is almost no radial growth in the basal diameter of shoots after they are out of the ground [12], the height growth of shoots may also be affected by chlorophyll.

One common management strategy for bamboo forests is to eliminate the potential negative effects of interspecific competition, meaning the removal of competing trees [21]. Studies have shown that different forest canopies reduce photosynthetically active radiation (PAR), red light, blue light, and far-red light (FR) in the forest due to the absorption or reflection of solar radiation [22–24]. Light is the most critical factor affecting plant growth and development [25,26], and its quality regulates plant morphology through signal transduction [27–30]. Previous studies mainly studied the effects of bamboo forest density, fertilization, and coverage on shoot quality [10,31]. However, little is known about whether the transformation of mixed bamboo forests into pure bamboo forests has an effect on the appearance quality of shoots.

Square bamboo, *Chimonobambusa utilis* (Keng) P. C. Keng, is widely planted in Southwest China for its nutritional value [32]. Herein, three types of bamboo forests were randomly selected based on canopy differences: evergreen broad-leaved forest with bamboo under-story (EBF), evergreen and deciduous broad-leaved mixed forest with bamboo understory (MBF), and pure bamboo forest (PBF). This study aimed to explore the impact of bamboo forest conversion on shoot appearance quality, elucidating the contributions of external factors (canopy structures, environmental factors, and mother bamboo structures) and internal factors (pigments and cells). The overarching goal is to enhance or preserve the taste and nutritional quality of bamboo shoots, concurrently improving their visual appeal. The specific hypotheses of the research were as follows: (i) the fresh mass, basal diameter, and height of shoots would significantly increase in PBF; (ii) the larger aboveground structure of mother bamboo, along with an increase in the length of rhizome and the number rhizome internodes (NRI), would be the dominant factors affecting the diameter thickening of shoots; (iii) the light factor and chlorophyll content of shoots would be the main factors affecting the height elongation of shoots.

2. Materials and Methods

2.1. Study Area and Experimental Design

The study was carried out in Nanchuan District, Chongqing, China (30.36° N, 119.47° E; Figure 1A). The climatic condition belongs to the subtropical temperate monsoon climate, the mean annual temperature is 8.3 °C, and the mean annual rainfall is 1390.5 mm. Soils are mainly yellow earth and mountain yellow-brown earth. The distribution altitude of *C. utilis* ranges between 1400 and 2252 m with various vegetation types.

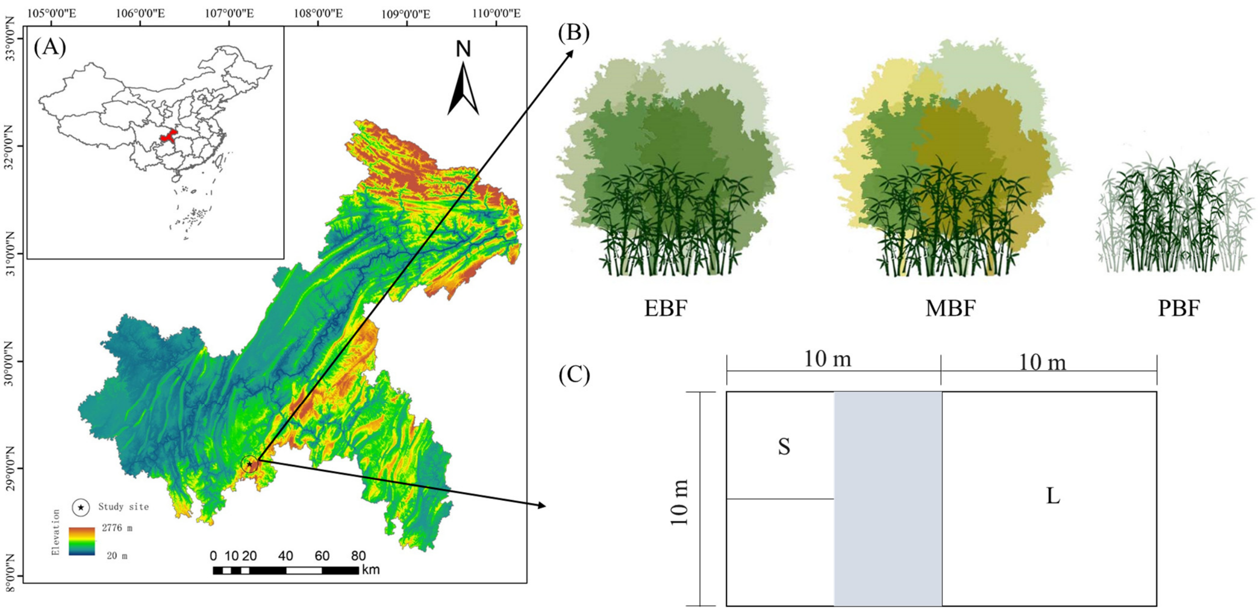

Figure 1. Experimental location and plot design. (**A**) Location of the sample site; (**B**) different forest types; (**C**) experimental plot design (the gray area indicates the experimental buffer zone). S is the bamboo shoot collection plot; L is the mother bamboo collection plot. Note: S: small plot; L: large plot.

C. utilis is a bamboo with a culm as high as 10 m and a diameter of about 2–4 cm; its shoots emerge in autumn. Three types of bamboo forest plots were selected in July 2021 (Figure 1B). The division of the three types of bamboo forest sample plots was based on the characteristics of canopy tree species and the proportion of the tree coverage. The proportion of evergreen broad-leaved tree canopy coverage was around 70%, which was defined as EBF; the proportion of deciduous broad-leaved trees coverage was around 30%, and total coverage was around 70%, which was defined as MBF (Figure 1B). The management pattern of the three types of bamboo forests was first implemented in 2011, such that the EBF and MBF were extensively managed after cutting off some canopy trees and understory shrubs, whereas the PBF was formed by cutting off canopy trees from evergreen broad-leaved trees and understory shrubs, and then every year after, all old bamboos and weak bamboos were cut off from the three forests. The geographic information and characteristics of the tree canopy of each plot are shown in Table S1. The numbers of EBF, MBF, and PBF plots were 5, 5, and 6, respectively (Figure 1C). The distance between each plot was greater than 20 m to ensure the independence of each plot. The L area of the plot was the mother bamboo collection area, determining their morphological factors. The small plot was the bamboo shoot collection area, and the gray area was the transition zone to reduce the influence of the mother bamboo collection on the development of shoots. The experiment was carried out at the early stage of shoot development to avoid interference with shoot growth and collection.

2.2. Environmental Factors

The photosynthetic photon flux density of blue light (400 nm–499 nm), red light (600 nm–699 nm), and FR light (700 nm–780 nm), as well as PAR, above each shoot from each plot S was measured using a portable spectrometer with a display (Rainbow light, MR-16-PPF, Rainbow Light Technology Co., Ltd., Taiwan, China) from 3 to 5 October 2021. Between the hours of nine in the morning and three in the afternoon, we took these measurements every two hours.

The soil around the bamboo rhizomes marked with shoots in each plot labeled S was collected on 6 October 2021 and brought back to the laboratory to determine the physical and chemical properties. Soil total carbon and total nitrogen were determined with an element analyzer (Vario EL cube, Heraeus Elementar, Hanau, Germany). Soil pH was measured using a pH meter (Mettler Toledo, FE20, Mettler-Toledo Instruments Co., Ltd., Shanghai, China) with a mixture of soil and deionized water at 1:2.5 (*w*/*w*). On 6 October 2021, when the three-parameter instrument was measuring soil temperature and humidity, the battery of the three-parameter instrument suddenly failed and could not work. On 4 October 2022 (a sunny day), we took another three-parameter instrument (LD-WSY, Leander Intelligent Technology Co., Ltd., Shandong, China) that could work properly to supplement the measurement of soil temperature and humidity. The soil temperature and soil moisture of 6 sites were randomly measured with the three-parameter instrument in the S plot.

The canopy was photographed 4 times repeatedly with a fisheye camera (Canon EOS 50D camera, Tokyo, Japan; Sigma EX DC 4.5 mm fisheye lens, Kanagawa, Japan) at the center of each plot labeled S on 10 October 2021, with the shooting height set to 1 m, the lens level maintained, and the compass pointed in the north direction. The images used were stored in JPG format. The HemiView digital plant canopy analysis system (Delta-T Devices Ltd., Cambridge, UK) was used to analyze canopy photos, and the canopy structure (canopy openness, mean leaf angle, and leaf area index) and understory light factors (scattered light, SL; direct light, DL) were measured.

2.3. Structural Factors of Mother Bamboos

From 2-year-old to 4-year-old mother bamboos, three mother bamboos of each age were randomly collected in each L area plot in August 2021. The mother bamboos' height and diameter at breast height (MDBH) were measured with a steel tape and a chest diameter ruler. All the mother bamboo rhizomes and rhizome roots were taken out from three soil plots of 50 cm × 50 cm that were randomly set up in each large-area plot on 4 September 2021. The number of rhizome internodes was counted. Rhizome length and rhizome diameter were measured with a steel measuring tape and a diameter at breast height ruler. Rhizome biomass and rhizome root biomass were measured with an electronic scale.

Aggregation index (AI) was calculated using the formula [33] shown in (1).

$$\mathrm{AI} = \frac{\frac{1}{C}\sum_{i=1}^{C} ri}{\frac{1}{2}\sqrt{\frac{A}{C}}} \tag{1}$$

AI is the aggregation index, *ri* represents the distance from the *i*-center bamboo to its nearest neighbor, *A* represents the plot area, and *C* represents the total number of bamboo in the plot.

2.4. Anatomical Structure of Bamboo Shoots

The base of bamboo shoots was collected and cut into 1 cm × 1 cm squares and stored in FAA (70% ethanol, acetic acid, and formaldehyde, 18:1:1 (*v*/*v*/*v*)) fixative on October 6th of 2021. The squares were divided into sections along their longitudinal axis and radial axis by hand sectioning. The sections were stained with 1% safranin and 0.1% fast green solution [9]. The section with successful staining and clear tissue from each sample was selected for observation and photographed with a 20 × objective lens of a Nikon E-Ci microscope (Nikon, Tokyo, Japan); each section was randomly photographed 5 times and saved. The software ImageJ (1.53 n, National Institute of Mental Health, Maryland, USA) (https://imagej.nih.gov/ij/index.html, accessed on 23 November 2021) was used to determine the number and length of parenchyma cells on the radial and longitudinal axes, as parenchyma cells account for a large part of bamboo shoot tissue, and the scale conversion was 0.24 µm/px. For radial axis sections, the diameter of 10 parenchyma cells in each photo was randomly measured, and the area of parenchyma tissue was selected with an "irregular selection frame". The number of parenchyma cells in each photo was calculated according to the area of a single parenchyma cell.

On the longitudinal sections, the longitudinal lengths of 10 parenchyma cells in each photo were randomly measured. Three columns of parenchyma cell length were randomly selected to calculate the number of cells per column. Accordingly, the number of parenchyma cells per 100 μm was calculated.

2.5. Appearance Qualities and Pigment Contents of Bamboo Shoots

The shoots in this study are usually collected as a commodity with a height of about 30 cm. This means that the starting height of shoots needed to be established according to our research objectives. According to China's 2021 weather forecast, it was predicted that the period from 1 October 2021 to 6 October 2021 would be sunny, while the weather would turn cloudy on 7 October. Therefore, the light factor could not be determined. Before this work, we observed that the optimum height for shoots to grow to 30 cm in about 5 days was about 5–7 cm, so we selected the initial height of shoots as 5–7 cm.

A total of 96 shoots, 6 shoots with a height of 5–7 cm from the excavation were randomly selected from each plot labeled S for labeling on 1 October 2021. All shoots were collected and brought back to a temporary refrigerator on 6 October. The height was measured with steel tape, the basal diameter was measured with a vernier caliper, and the fresh mass was measured with the electronic scale (removing the shoot shells).

The colored tissues of the shoots were removed, chopped, and mixed, randomly weighed 0.1 ± 0.05 g, and placed in a centrifuge tube with 95% ethanol and a little dilution of 10 mL of $CaCO_3$. After the setup was stocked in the dark for 24 h, it was rotated at 5000 rpm for 6 min, and then, the supernatant was separated and prepared for measurement. Based on the maximum absorption peak of chlorophyll in 95% ethanol, the absorption values at 665 nm, 649 nm, and 470 nm were measured with an ultraviolet–visible spectrophotometer (Shimazu, UV2700, Tokyo, Japan). The contents of chlorophyll *a* and carotenoid were calculated using Equations (2) and (3), where the volume of the supernatant extracted, F, is the fresh mass of the samples [34]:

$$\text{chlorophyll } a = \frac{(13.95A665 - 6.88A649) \times V}{F} \tag{2}$$

$$\text{carotenoid} = \frac{\left(1000A470 - 2.05\left(\frac{(13.95A665-6.88A649)\times V}{F}\right) - 114.8\frac{(24.96A649-7.32A665)*V}{F}\right) \times V}{F} \tag{3}$$

2.6. Taste and Nutritional Quality of Bamboo Shoots

The soluble protein content was measured using the Coomassie brilliant blue G-250 method [35]. The protein exhibited a maximum ultraviolet absorption peak at 595 nm, and the protein content of the shoots was quantitatively analyzed. The fresh shoots were ground into a powdery form, and 0.5 g of this powder was placed into a centrifuge tube. Then, 8 mL of distilled water was added and left at room temperature for 0.5–1 h to ensure full extraction. The mixture was then centrifuged at 4000 r/min for 20 min. The supernatant was diluted to a volume of 10 mL to obtain a soluble protein solution. The soluble protein content was determined using an ultraviolet–visible spectrophotometer (Shimazu, UV2700, Tokyo, Japan) at 595 nm.

Additionally, the content of cellulose was determined by acid hydrolysis–anthrone colorimetry [36]. A 0.02 g sample of dried shoot powder was placed in a 20 mL test tube. A volume of 6 mL of 60% H_2SO_4 was added to the sample and digested for 30 min. Thereafter, the digested cellulose solution was then transferred to a 25 mL volumetric flask and diluted to the mark with 60% H_2SO_4. After shaking, the solution was transferred to a 50 mL centrifuge tube and centrifuged at 5000 r/min for 10 min. A volume of 0.5 mL of the supernatant was transferred to a 10 mL centrifuge tube and diluted to 10 mL to obtain a cellulose extract. A volume of 2 mL of the cellulose extract was transferred to a test tube with a stopper; 0.5 mL of 2% anthrone reagent was added, followed by the addition of 5 mL of concentrated H_2SO_4 along the tube wall. With the stopper inserted, the tube was shaken and left to stand for 12 min. The absorbance value of the sample was measured at a wavelength of 620 nm using an ultraviolet spectrophotometer (Shimazu, UV2700, Tokyo, Japan).

The lignin content was determined by the acetyl bromide method [37]. A 5 mg sample of dried shoot powder was accurately weighed and placed in a 15 mL centrifuge tube. A 25% acetyl bromide–glacial acetic acid solution was quickly prepared and transferred to a sealed reagent bottle. Volumes of 1 mL of 25% glacial acetic acid solution and 0.1 mL of 70% perchloric acid solution were added to the sample in sequence, and the reaction was carried out in a 70 °C constant-temperature water bath for 30 min, with shaking every 10 min. After natural cooling, 1 mL of 2 mol/L NaOH was added to stop the reaction, and the volume was adjusted to 10 mL with glacial acetic acid. After shaking, the absorbance value was measured with an ultraviolet–visible spectrophotometer (Shimazu, UV2700, Tokyo, Japan) at a wavelength of 280 nm.

2.7. Statistical Analysis

To ensure the robustness of our analysis, we conducted preliminary tests using Shapiro–Wilk and Levene tests in SPSS software (v22.0, IBM Inc., Chicago, IL, USA) to assess the normality and homogeneity of variance of the data. Then, a one-way analysis of variance (ANOVA) was used to test the significance of canopy structure, understory light factor, understory soil factor, mother bamboo factor, shoot pigment content, shoot tissue and shoot quality among three different bamboo forest types. The statistical significance was determined at $p < 0.05$.

For a comprehensive evaluation of the morphological impacts of bamboo shoots, we utilized the "randomForest" R package [38] (in the R 4.2.3) to rank and identify the influencing factors. This involved employing the random forest model to assess the effects of various factors (the canopy structure, light factors, soil factors, structural factors of mother bamboos, pigment content, cell number, and cell length of shoots) on the basal diameter and height of bamboo shoots. To elucidate the impact of these important factors on the shoots' height and basal diameter, we employed the linear mixed effect model using the "lmerTest" of the R package (in the R 4.2.3). In each model, factors with an impact exceeding 5% (as determined by the random forest model) were considered fixed effects, while the forest type was fitted as random effects. The significance of fixed effects was evaluated using the maximum likelihood method. We initiated a full model with all variables as fixed effects and iteratively simplified it to a final model containing only significant variables ($p < 0.05$). Model simplification was based on the marginal $R^2{}_m$ (the variance explained by fixed factors alone) and conditional $R^2{}_c$ (the variance explained by fixed and random factors) calculated using the package "glmm.hp" [39]. To address discrepancies in sample sizes, particularly for the canopy structure and mother bamboo factors, we calculated the average values of canopy structure, aboveground structure, and underground structure of mother bamboo for each plot and repeated this six times. Similarly, we averaged values for cell diameter, length, and cell number in the radial and axial systems of each shoot.

3. Results

3.1. Canopy Structures, Mother Bamboo Structures, and Understory Environmental Factors

Affected by management and bamboo forest types, there were some differences in the influencing factors in the three bamboo forests (Table 1). Compared with EBF, the canopy openness and leaf area index of PBF did not change, but the mean leaf angle increased significantly ($p < 0.001$, Table 1). Also, compared with MBF, the mean leaf angle and leaf area index of PBF were significantly higher ($p < 0.001$), but canopy openness was significantly lower than MBF ($p < 0.001$). The MDBH ($p < 0.01$) and rhizome biomass ($p < 0.001$) of PBF were the highest, while the density ($p < 0.001$) and height ($p < 0.01$) of mother bamboos were the lowest. The AI values ($p < 0.001$), rhizome root biomass ($p < 0.05$), and rhizome diameter ($p < 0.001$) of PBF were significantly higher than those of EBF. The rhizome length (RL) of PBF decreased significantly ($p < 0.05$) compared with that of EBF and MBF. There was no significant difference in the NRI in the three bamboo forests. The light factors of

MBF were the largest ($p < 0.05$), which was significantly different from EBF (except the DL) and PBF. There was no significant difference in other light factors between EBF and PBF, except that the SL of EBF was significantly smaller than that of PBF ($p < 0.001$). The soil temperature of MBF ($p < 0.05$), soil moisture of PBF ($p < 0.001$), and total N and total C of EBF were the highest ($p < 0.001$).

Table 1. Canopy structures, mother bamboo structures, and understory environmental factors of different types of forests (means ± SE; n = 6).

Impact Factors		Forest Types		
		EBF	**MBF**	**PBF**
Canopy structures	CO (%)	10.67 ± 0.28 b	13.08 ± 0.35 a	10.58 ±0.17 b
	MLA (°)	40.53± 2.64 b	34.39 ± 1.98 c	55.98 ± 1.64 a
	LAI	2.34 ± 0.07 a	1.98 ± 0.05 b	2.47 ± 0.03 a
Mother bamboo structures	MDBH (cm)	1.59 ± 0.03 c	1.82 ± 0.03 b	2.01 ± 0.06 a
	MH (m)	3.88 ± 0.07 a	3.88 ± 0.06 a	3.52 ± 0.13 b
	Density (culms hm^{-2})	42,640.00 ± 2592.98 a	43,760.00 ± 1773.74 a	26,066.67 ± 1978.33 b
	AI	0.84 ± 0.02 b	0.97 ± 0.01 a	0.99 ± 0.02 a
	NRI (internode m^{-2})	55.33 ± 1.84	58.02 ± 1.54	57.13 ± 0.78
	RB (g m^{-2})	430.96 ± 23.96 c	643.08 ± 45.52 b	924.32 ± 49.72 a
	RL (cm)	38.18 ± 0.70 a	38.16 ± 0.33 a	36.33 ± 0.47 b
	RD (cm)	0.97 ± 0.05 b	1.11 ± 0.08 a	1.07 ± 0.06 a
	RRB (g m^{-2})	109.8 ± 5.92 b	132.56 ± 8.44 a	117.36 ± 3.36 ab
Light parameters	B (μmol m^{-2} s^{-1})	5.50 ± 1.24 b	19.51 ± 4.76 a	5.31 ± 0.63 b
	R (μmol m^{-2} s^{-1})	8.97 ± 2.18 b	31.88 ± 8.04 a	8.14 ± 0.99 b
	FR (μmol m^{-2} s^{-1})	18.78 ± 1.70 b	41.18 ± 6.39 a	28.40 ± 1.28 b
	R/FR	0.38 ± 0.04 b	0.54 ± 0.06 a	0.26 ± 0.02 b
	PAR (μmol m^{-2} s^{-1})	22.54 ± 5.20 b	79.31 ± 19.57 a	21.21 ± 2.47 b
	DL (mol m^{-2} yr^{-1})	1491.97 ± 53.05 ab	1658.89 ± 70.21 a	1420.82 ± 55.51 b
	SL (mol m^{-2} yr^{-1})	1416.37 ± 26.57 c	1671.50 ± 23.37 a	1651.68 ± 29.69 b
Soil factors	pH	4.89 ± 0.09	4.74 ± 0.08	4.90 ± 0.05
	ST (°C)	17.68 ± 0.15 b	18.08 ± 0.06 a	17.71 ± 0.11 b
	SM (%)	15.92 ± 0.97 b	15.97 ± 0.64 b	25.31 ± 1.49 a
	TN (g kg^{-1})	17.01 ± 1.00 a	12.27 ± 0.85 b	10.99 ± 0.62 b
	TC (g kg^{-1})	200.91 ± 6.70 a	150.95 ± 7.42 b	134.68 ± 7.47 b
	C/N	12.50 ± 0.43	12.80 ± 0.32	12.34 ± 0.17

Different lowercase letters indicate significant differences between different bamboo forest types ($p < 0.05$). Notes: CO: canopy openness; MLA: mean leaf angle; LAI: leaf area index; MDBH: diameter at breast height of mother bamboos; MH: height of mother bamboos; AI: aggregation index; NRI: number of rhizome internodes; RB: rhizome biomass; RL: rhizome length; RD: rhizome diameter; RRB: rhizome root biomass; B: blue light; R: red light; FR: far-red light; R/FR: red to far-red light ratio; PAR: photosynthetically active radiation; DL: direct light; SL: scattered light; ST: soil temperature; SM: soil moisture; TN: total N; TC: total C; C/N: total C to total N ratio.

3.2. The Number and Size of Tissue Cells and Pigment Contents of Bamboo Shoots

The change in bamboo forest management did not change the growth of shoot parenchyma cells in the axial system and radial system (Figure 2). There was no significant difference in the number and size of shoot cells under the three types of forests. There was no significant difference in chlorophyll *a* contents between the EBF shoots and PBF shoots, while the chlorophyll *a* contents in the EBF shoots and PBF shoots were significantly different from that in MBF shoots ($p < 0.05$, Figure 3A). The difference in carotenoid contents in different types of forests were consistent with the difference in chlorophyll *a* contents in different types of forests ($p < 0.001$, Figure 3B).

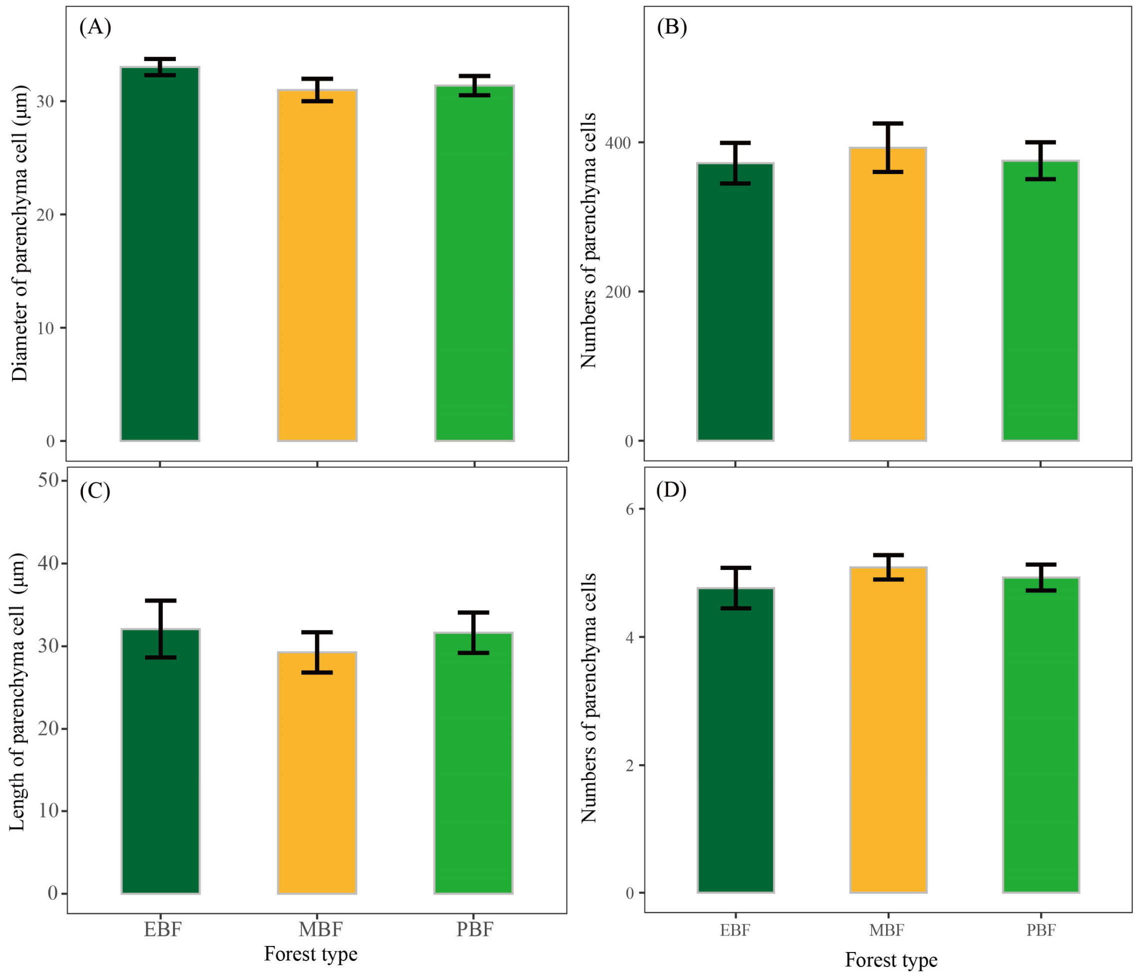

Figure 2. Number and size of bamboo shoot tissue cells (means ± SE; n = 6). The diameter of parenchyma cells (**A**) and number in regions of 10,242 μm^2 (**B**) in the radial system, and the length of parenchyma cells (**C**) and number per 100 μm (**D**) in the axial system.

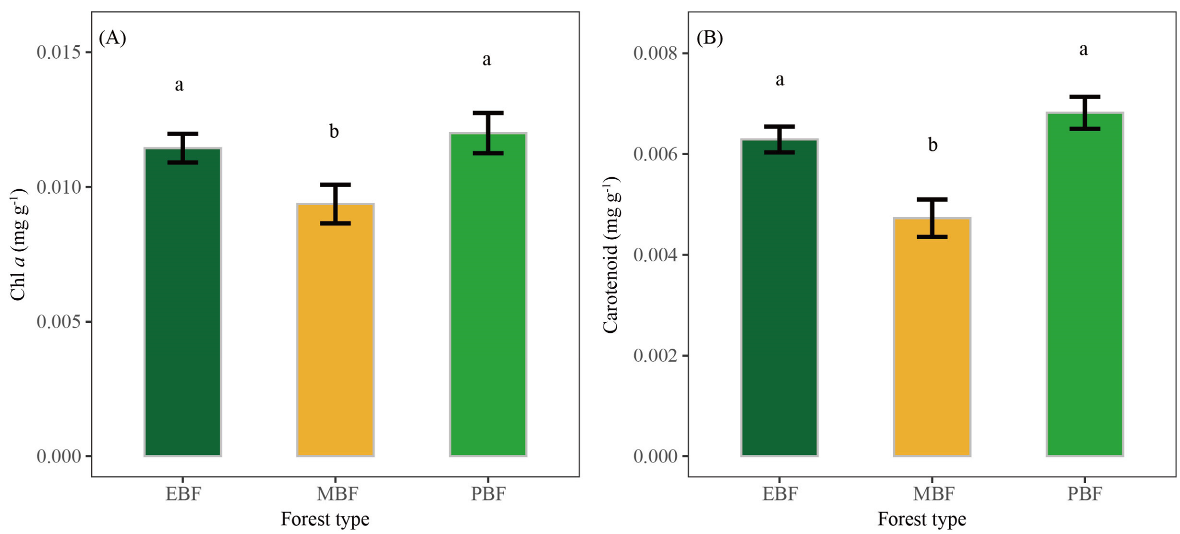

Figure 3. Pigment contents of bamboo shoots in different types of bamboo forests (means ± SE; n = 6). (**A**) Chlorophyll *a* content of bamboo shoots; (**B**) carotenoid content of bamboo shoots. Different lowercase letters indicate significant differences between different types of bamboo forests ($p < 0.05$). Note: Chl *a*: chlorophyll *a*.

3.3. The Appearance Quality of Bamboo Shoots

The fresh mass of shoots of PBF was 29.15 g and heavier than that of EBF by 10.37 g, there was also no significant difference with that of MBF (Figure 4A). There was no significant difference between the heights of shoots of the three types of forests (Figure 4B). The basal diameter of shoots of PBF was 1.89 cm and significantly larger than that of EBF by 0.27 cm ($p < 0.05$), but there was no significant difference compared with that of MBF. The basal diameter of shoots of MBF was larger than that of EBF by 0.35 cm ($p < 0.01$, Figure 4C).

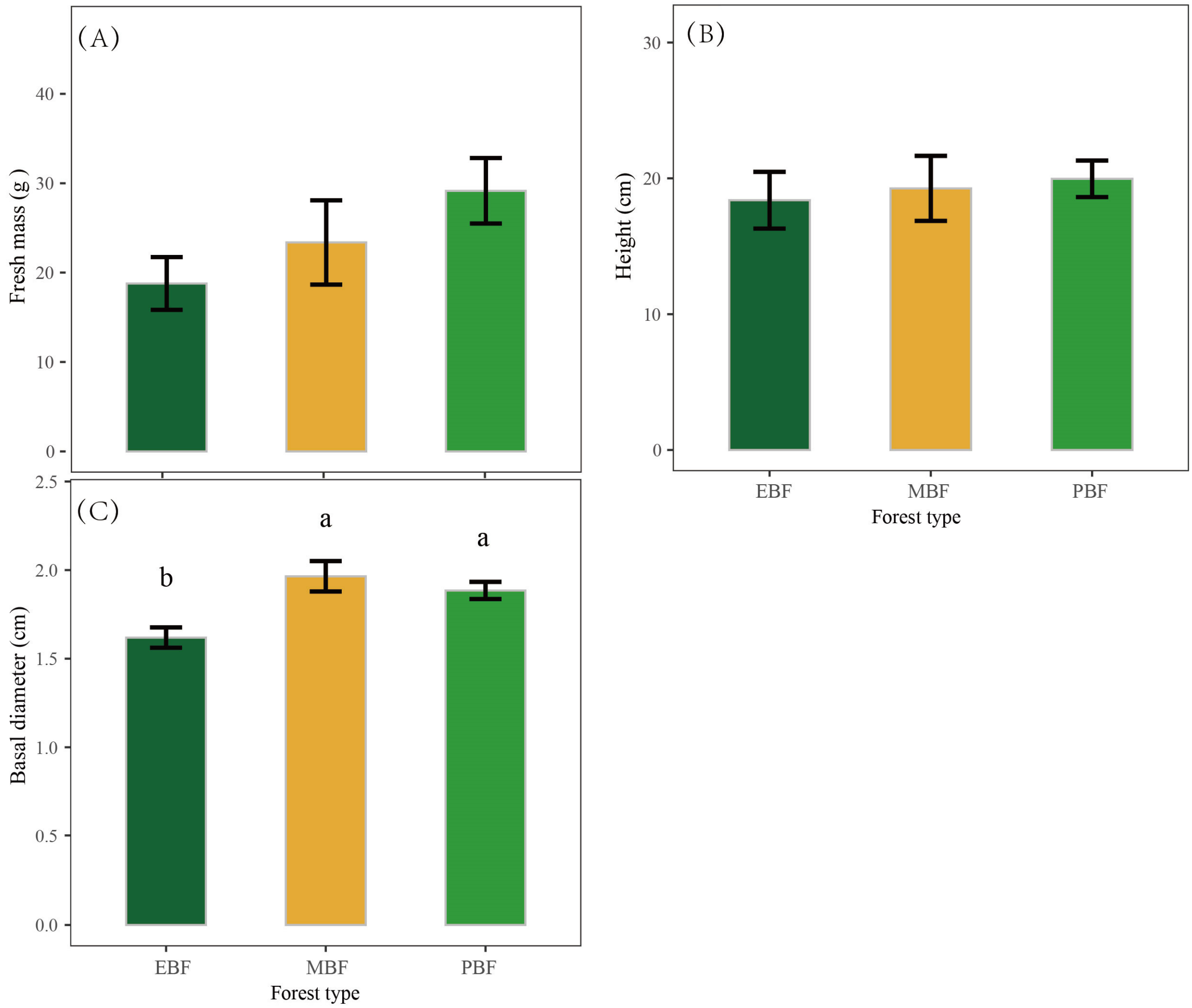

Figure 4. The appearance quality of bamboo shoots (means ± SE; $n = 6$). (**A**) Fresh mass of bamboo shoots; (**B**) height of bamboo shoots; (**C**) basal diameter of bamboo shoots. Different lowercase letters indicate significant differences between different types of bamboo forests ($p < 0.05$).

3.4. The Taste and Nutritional Quality of Bamboo Shoots

There was no significant difference in the protein content of shoots between EBF and PBF, at 4.31 mg/g and 4.36 mg/g, respectively. The protein content of shoots in MBF was 3.89 mg/g, which was significantly lower than that of EBF and PBF ($p < 0.001$). The cellulose contents of shoots in EBF, MBF, and PBF were 480.37 mg/g, 478.75 mg/g, and 480.47 mg/g, respectively. The lignin contents of shoots in EBF, MBF, and PBF were 105.47 mg/g, 107.68 mg/g, and 104.57 mg/g, respectively. There was no significant difference in the cellulose and lignin contents of shoots in the different bamboo forests (Figure 5).

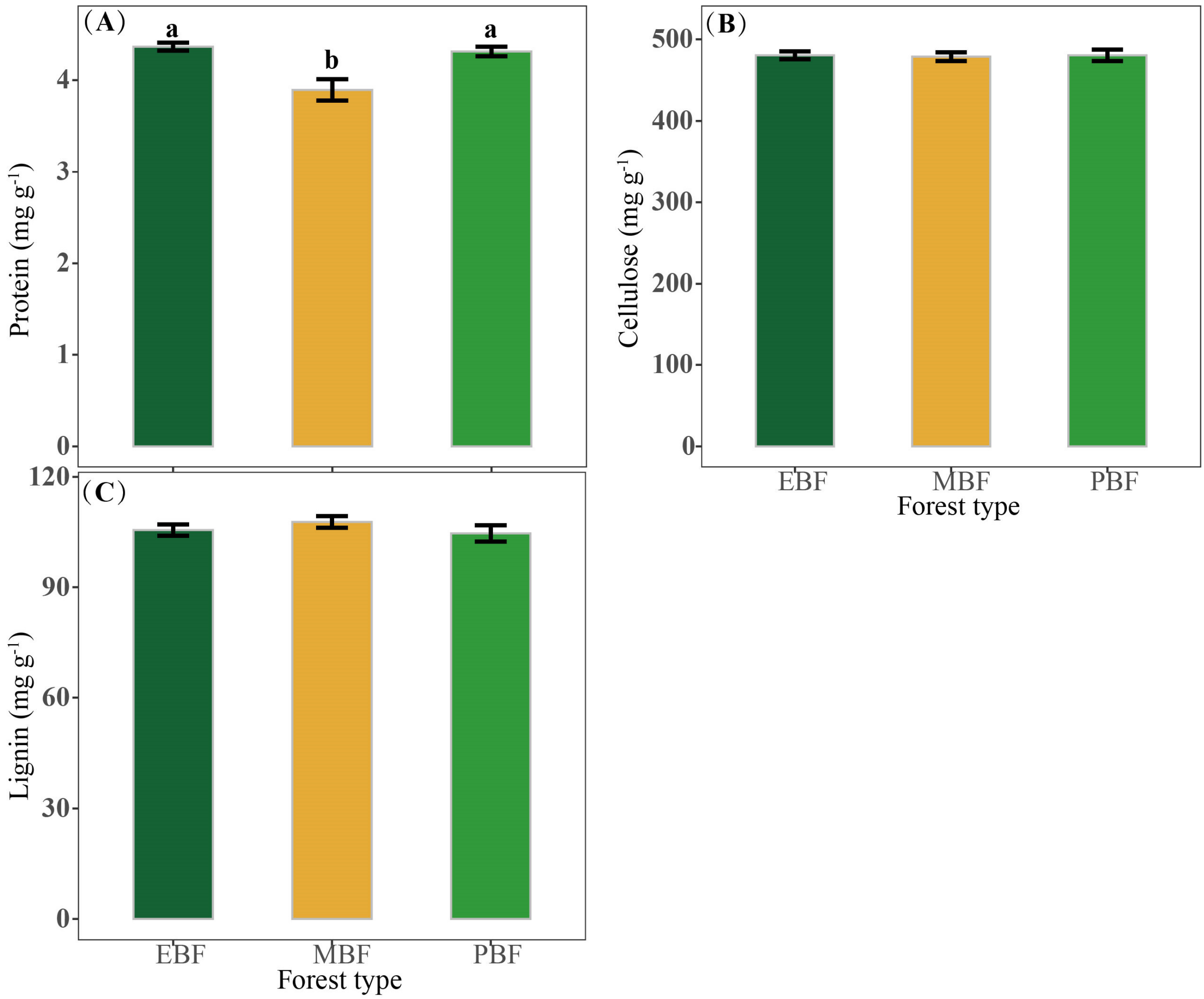

Figure 5. Taste and nutritional quality of bamboo shoots in different bamboo forests. (**A**) Protein content; (**B**) cellulose content; (**C**) lignin content (means ± SE; $n = 6$). Different lowercase letters indicate significant differences between different types of bamboo forests ($p < 0.05$).

3.5. Correlations between the Appearance Quality of Bamboo Shoots and Influencing Factors

The fresh mass of the shoots was significantly positively correlated with the height and basal diameter of the shoots ($p < 0.01$; Figure 6). The basal diameter of the shoots was significantly positively correlated with NRI ($p < 0.01$), RDPC, and RL ($p < 0.05$) and significantly negatively correlated with RNPC ($p < 0.01$). The height of shoots was significantly positively correlated with the chlorophyll *a* content, carotenoid content, and ALPC ($p < 0.01$) but significantly negatively correlated with ANPC ($p < 0.01$). In addition, the fresh mass of shoots and the height of shoots were significantly positively correlated with the cellulose content and lignin content ($p < 0.01$), but not with protein content ($p > 0.05$). The basal diameter of shoots was not correlated with the contents of protein, cellulose, and lignin ($p > 0.05$).

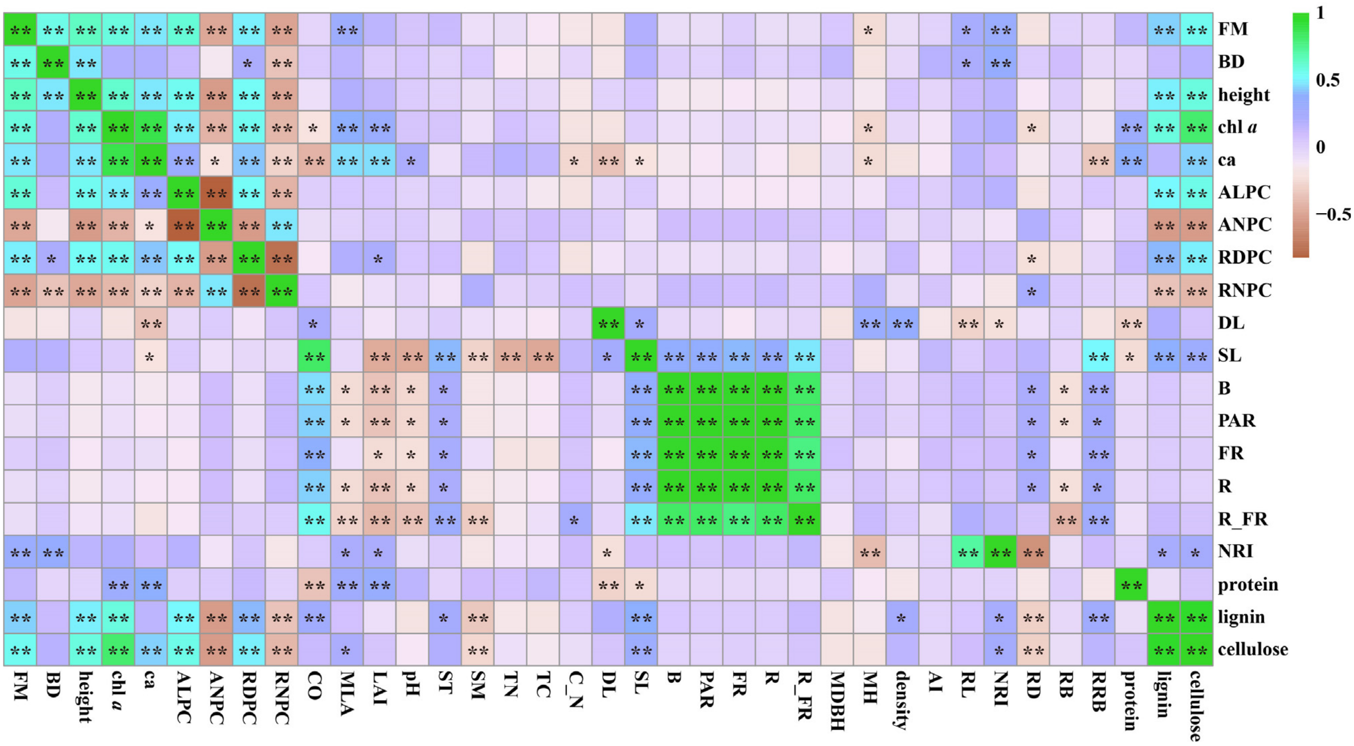

Figure 6. Correlations between appearance quality of bamboo shoots and influencing factors (* for $p < 0.05$, ** for $p < 0.01$). Notes: FM: fresh mass of bamboo shoots; BD: basal diameter of bamboo shoots; chl *a*: chlorophyll *a*; ca: carotenoid; ALPC: parenchyma cell length in the axial system; ANPC: parenchyma cell number in the axial system; RDPC: parenchyma cell diameter in the radial system; RNPC: parenchyma cell number in the radial system; CO: canopy openness; MLA: mean leaf angle; LAI: leaf area index; ST: soil temperature; SM: soil moisture; TN: total N; TC: total C; C_N: total C to total N ratio; DL: direct light; SL: scattered light; B: blue light; PAR: photosynthetically active radiation; FR: far-red light; R: red light; R_FR: red to far-red light ratio; MDBH: diameter at breast height of mother bamboos; MH: height of mother bamboos; AI: aggregation index; RL: rhizome length; RD: rhizome diameter; NRI: number of rhizome internode; RB: rhizome biomass; RRB: rhizome root biomass.

3.6. The Predictors of Bamboo Shoot Morphology

The important predictors for the basal diameter of shoots were RNPC, NRI, RDPC, and FR according to the random forest model (Figure 7A), of which the importance value of RNPC was 15.85%, and the NRI was 9.00%. The chlorophyll *a* content (importance value = 29.86%), ALPC (importance value = 21.35%), ANPC (importance value = 14.54%), and carotenoid content (importance value = 11.13%) were the important predictors for the height of shoots (Figure 7B).

According to the linear mixed effect model, RNPC and NRI explained 19.05% of the variance in the basal diameter of shoots (Figure 8A). The effect of NRI had a positive effect on the basal diameter, explaining 8.11% ($p < 0.01$), while the RNPC had a negative effect on the basal diameter of shoots and explained 10.94% ($p < 0.001$). Based on the linear mixed effects model, the main influencing factors explained 47.53% of the variance in the height of shoots (Figure 8B). The effects of chlorophyll *a* content ($p < 0.001$) and ALPC ($p < 0.001$) on the height of shoots were positive, as shown in Figure 8B. The chlorophyll *a* content and the ALPC explained 29.06% and 18.47% of the variance for the height of shoots, respectively.

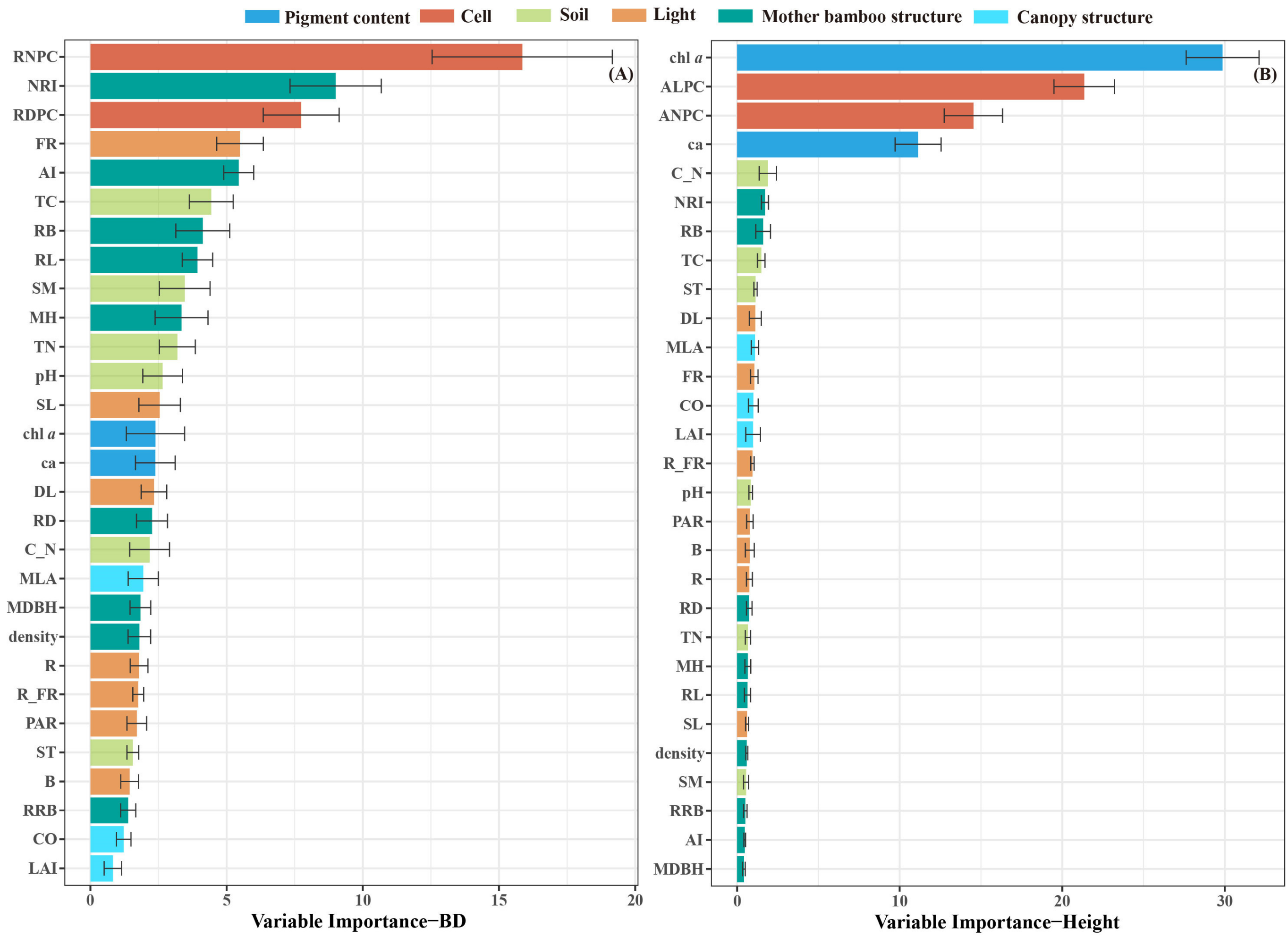

Figure 7. The rank results of the random forest model feature importance for the morphology of bamboo shoots ((**A**) the basal diameter of bamboo shoots; (**B**) the height of bamboo shoots). Notes: BD: basal diameter of bamboo shoots; chl *a*: chlorophyll *a*; ca: carotenoid; ALPC: parenchyma cell length in the axial system; ANPC: parenchyma cell number in the axial system; RDPC: parenchyma cell diameter in the radial system; RNPC: parenchyma cell number in the radial system; ST: soil temperature; SM: soil moisture; TN: total N; TC: total C; C_N: total C to total N ratio; SL: scattered light; DL: direct light; B: blue light; R: red light; FR: far-red light; R_FR: red to far-red light ratio; MDBH: diameter at breast height of mother bamboos; MH: height of mother bamboos; AI: aggregation index; RB: rhizome biomass; RL: rhizome length; RD: rhizome diameter; NRI: number of rhizome internode; RRB: rhizome root biomass; CO: canopy openness; MLA: mean leaf angle; LAI: leaf area index.

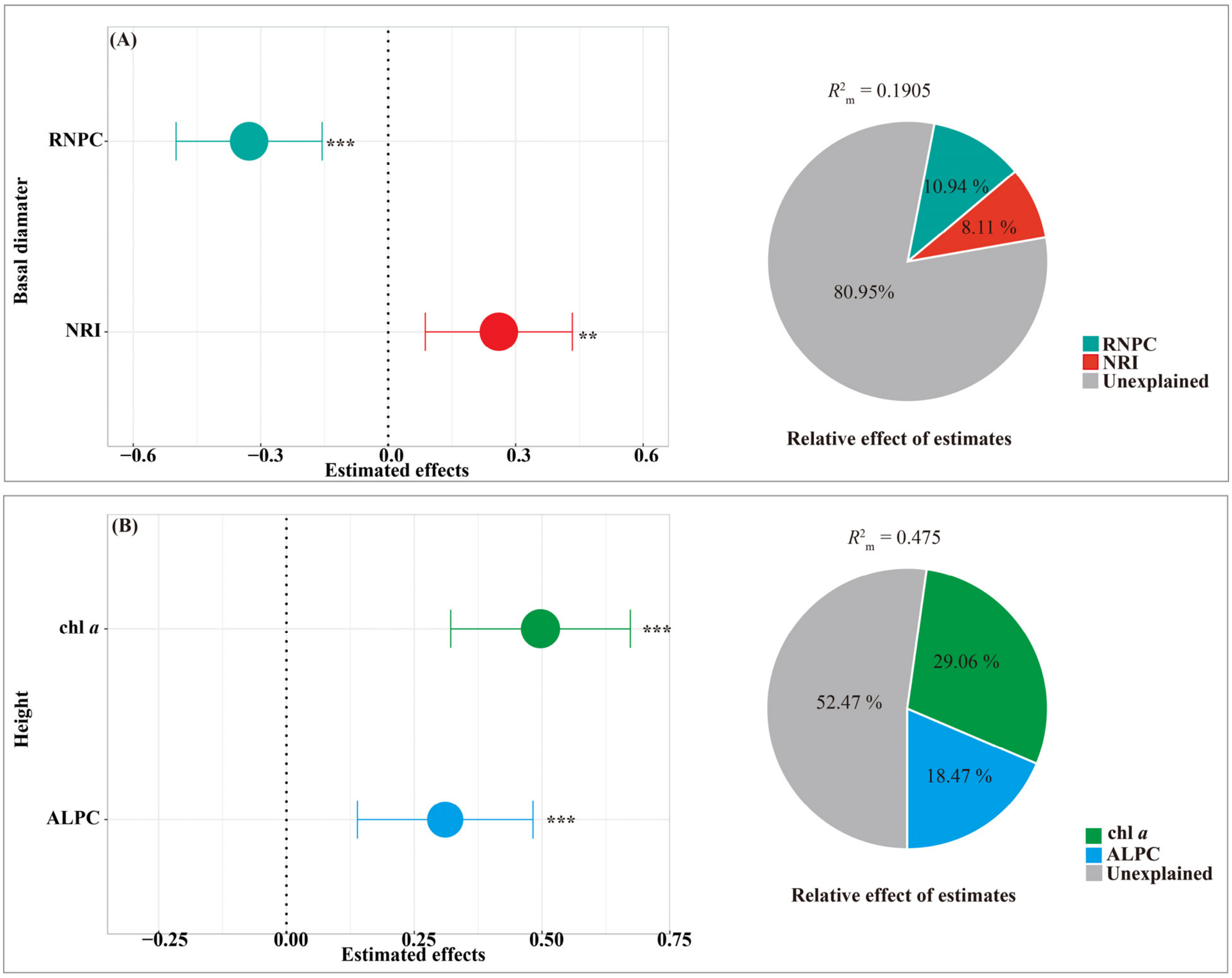

Figure 8. The linear mixed effect models of influencing factors on bamboo shoot morphology ((**A**) for the basal diameter of bamboo shoots and (**B**) for the height of bamboo shoots) (** for $p < 0.01$; *** for $p < 0.001$). Notes: RNPC: parenchyma cell number in the radial system; NRI: number of rhizome internode; chl *a*: chlorophyll *a*; ALPC: parenchyma cell length in the axial system.

4. Discussion

4.1. The Effects of Removing Competitive Wood on the Quality of Bamboo Shoots

In this study, the effect of removing competitive wood on the appearance quality of shoots and the key factors were discussed from the perspective of the growth characteristics of shoots. From the perspective of improving the taste and nutritional quality of shoots, the optimal management strategy for bamboo forests was put forward.

The results of our research partially supported hypothesis i, because the basal diameter of shoots increased significantly, but the height and fresh mass of shoots in PBF did not change (Figure 4). The basal diameter of shoots was no significant correlation with the taste and nutritional quality of shoots, while the fresh mass and height of shoots were significantly positively correlated with the cellulose and lignin content of shoots (Figure 6). Therefore, the effect of the high growth of shoots on the taste quality of shoots needs more attention. The soil nutrients of PBF significantly decreased (Table 1) in the study but did not reach the level of affecting the growth of bamboo forests, while the nutrient release rate of pure bamboo forest litter was slow due to the single nutrient source of litter in pure bamboo forests [40]. The high yield of PBF (Figure S1) and a large number of shoots were collected every year, which would lead to the transfer of a large number of chemical elements, resulting in a decrease in nutrient content in bamboo forests. This showed long-term management would be bound to cause soil degradation. Additionally, to improve the soil nutrients of bamboo plantations, large amounts of organic matter and chemical fertilizers were applied, which led to soil degradation [41], and the soil degradation [42] changed the quality of shoots [43]. Canopy trees (deep-rooted trees) could return the nutrients of the deep soil to the surface in the form of litter, which could satisfy the needs of the growth of shallow roots in bamboo forests and the maintenance of the quality of shoots. Hence, bamboo combined with canopy trees can be considered to achieve the sustainable management of bamboo forests.

4.2. The Effects of Influence Factors on the Basal Diameter of Bamboo Shoots

RL, NRI, and RDPC had a positive correlation with the shoot basal diameter, while RNPC had a significant negative correlation with the shoot basal diameter (Figure 6). However, the NRI and RNPC were the main factors affecting the regulation of shoot basal diameter (Figure 8A); this was partly consistent with hypothesis ii. The results of our study showed that the understory environmental factors had little effect on the basal diameter of shoots, especially the understory light factor. This might be due to the unique development model of shoots, which have no branches and blades before they become bamboo, and the nutrients developed are from the nearby mother bamboos and bamboo rhizomes [44,45]. While *C. utilis* is a kind of rhizome of monopodial and mixed bamboo, the shoots are far away from the mother bamboos, and the growth of the bamboo rhizomes as a nutrient storage organ has a greater impact on the basal diameter of shoots. Rhizomes store and allocate nutrients by increasing the length and number of rhizome segments rather than the diameter of bamboo rhizomes [16]. Therefore, RL and NRI were significantly positively correlated with the basal diameter of shoots (Figure 6). In this study, the basal diameter of shoots in PBF and MBF was the largest, while there was no difference in the NRI among the three forest types (Table 1), indicating that there were other factors affecting the basal diameter of shoots. The NRI had a negative correlation with the density of the mother bamboos (Figure 6), while [16] showed that after moso bamboo forest reforestation, the number of moso bamboo rhizomes was positively affected, along with the culms and biomass of the mother bamboos. This shows that the phenotypic plasticity of bamboo growth was relatively strong. Bamboo places organs in a more resource-rich environment [46], while there is resource competition among the mother bamboos [17]. Therefore, hypothesis ii was partially proved; the factors affecting the NRI need to be further studied.

The RNPC had a significant negative effect on the basal diameter of the shoots (Figure 8A), while RDPC had a significant correlation on the basal diameter of the shoots (Figure 6). RNPC was negatively regulated by the chlorophyll *a* content of shoots (Figure S3A), while RDPC was positively regulated by the chlorophyll *a* content of shoots (Figure S3B). However, the chlorophyll *a* content of shoots had no effect on the basal diameter of shoots (Figures 6 and 8A). Therefore, hypothesis ii was rejected; shoot cell factors had an important influence on the basal diameter of shoots, and the chlorophyll *a* content of shoots had an effect on the cells of the shoots, but the effect on the basal diameter of shoots was limited. Therefore, it is necessary to further understand the effect of influencing factors on the axial cell development of shoots.

4.3. The Effects of Influencing Factors on the Height of Bamboo Shoots

Shoot pigments, ANPC, and ALPC were significantly correlated with the shoot height (Figure 6), while the linear mixed effects model showed that the chlorophyll *a* content and ALPC principally promoted the height of shoots Figure 8B), which was partly consistent with hypothesis iii. It was discovered that, because the conversion of the canopy composition of bamboo forests changed (Table 1), the understory environmental factors had little effect on the height of shoots (Figures 6 and 8B), which was different from the morphological characteristics of plants promoted or inhibited by light quality regulation [47,48]. It was found that the growth of spruce and fir seedlings tended to appear in height rather than diameter under the same SL conditions [49]. However, there was no significant correlation between SL and the height of shoots in this study, and there was no secondary structure in the shoots. There may be three main reasons for this: the first reason is that the previous study was an indoor light control experiment; this experiment was conducted under natural light, and the proportion of light quality in natural light may have an uncertain effect on the morphology of shoots. The second is that the light factor measured in the experiment was measured every two hours, which may have been more affected by the time of measurement and the canopy structure and may be more suitable for the continuous monitoring of the light quality of a forest. The third reason is that the understory light factor did not directly affect the morphological structure of shoots but indirectly affected the morphological structure of shoots by affecting the chlorophyll *a* content of the shoots [19,20]. In our study, the elongation growth of the shoots was affected by the network regulation path of light and hormones on the formation of chloroplasts in the shoots, which is consistent with the study of Cackett et al. [19]. Chlorophyll includes chlorophyll *a* and chlorophyll *b*; however, only the effect of chlorophyll *a* on the height of shoots was proved in this study. Whether chlorophyll *b* also has an important effect needs further study.

The spectrum with a higher proportion of blue light has a positive effect on the accumulation of chlorophyll [50,51], while a low R/FR has a negative effect on the accumulation of chlorophyll [52]. The biosynthesis of carotenoids is affected by factors such as radiation intensity [53] and different R/FR ratios [54]. Except for the fact that the FR under the forest was not related to the average leaf angle, other light quality factors were significantly correlated with the canopy structures. However, we found that the light quality in this study had no effect on the pigment content of shoots, which was mainly affected by the canopy structure and SL and DL (Figure S4). This indicated that the canopy structure changed the SL and DL of different bamboo forests, and the SL and DL affected the chlorophyll *a* and carotenoid content of shoots. The chlorophyll a and carotenoid content of shoots affected the height of the shoots, which also answered hypothesis iii. The position of a tree in the canopy gap determines the amount of light received [55,56]. Leaf inclination is an important plant structural trait [57], which largely determines radiation interception [58]. The gap size of tree species composition [49], leaf area index, and leaf shape significantly reduce direct and scattered light in the lower canopy [59]. The EBF and PBF species in this study were evergreen tree species, while the canopy tree species of MBF were partly deciduous broad-leaved tree species. The leaf inclination angle of deciduous broad-leaved tree species is often an acute angle [57,60], resulting in different canopy openness, which also allows more light to reach the lower part of the canopy. This also showed that deciduous broad-leaved tree species as canopy species of bamboo forests may not be beneficial to the taste and nutritional quality of bamboo forests.

In this study, ALPC had a significant positive effect on the height of shoots (Figure 8B), which rejected hypothesis iii. The study also showed that ALPC was significantly positively correlated with cellulose and lignin content in shoots, while ANPC was significantly negatively correlated with cellulose and lignin content in shoots (Figure 6). Therefore, by increasing the ANPC of shoots, it could be beneficial to improve the taste quality of shoots. The carotenoid had a significant positive effect, and chlorophyll *a* content had a significant negative effect on the ANPC (Figure S3C). However, ALPC was regulated by shoot pigments, which was opposite to ANPC (Figure S3D). The carotenoid content of shoots had a significant positive effect on the protein content of shoots. The chlorophyll *a* content of shoots was significantly positively correlated with the content of cellulose and lignin in shoots (Figure S2). Therefore, increasing the content of carotenoid in shoots or reducing the content of chlorophyll *a* in shoots may be beneficial to improve or maintain the taste and nutritional quality of shoots. In this study, SL and mean leaf angle had significant positive effects on the chlorophyll *a* and carotenoid content of shoots, respectively (Figure S4A,B), while SL was positively correlated with canopy openness and negatively correlated with the leaf area index (Figure 6). Therefore, reducing the canopy openness and increasing the leaf area index of bamboo forest could help to reduce the chlorophyll *a* content of shoots, and increasing the mean leaf angle could help to increase the carotenoid content of shoots. Therefore, the different strategies of forest management (e.g., changing the forest structure and species component, reducing deciduous tree species, and retaining or transplanting tree species with larger leaf inclination angles) would be beneficial to improve the taste quality and nutritional quality of bamboo shoots.

5. Conclusions

The study was the first attempt to reveal the influence mechanism of common bamboo forest management strategies (competitive tree species removal) on improving the appearance quality of bamboo shoots. Our findings indicated that the appearance quality of bamboo shoots in pure bamboo forests significantly improved under the management strategy of removing competitive trees. The NRI and the chlorophyll *a* content of bamboo shoots were identified as the primary factors contributing to the basal diameter thickening and elongation growth of shoots, respectively. However, the chlorophyll *a* content of bamboo shoots exhibited a positive effect on the cellulose and lignin content of bamboo shoots, while the carotenoid content of bamboo shoots showed a positive influence on the protein content of bamboo shoots. In addition, we observed that increasing the bamboo canopy and mean leaf angle could assist in reducing the chlorophyll *a* content and enhancing the carotenoid content of shoots, thus contributing to the improvement in or maintenance of shoot quality. This study emphasized that, for the purpose of enhancing or maintaining the nutritional quality and taste quality of shoots, increasing the NRI, bamboo canopy, and mean leaf angle would be beneficial in improving the appearance quality of shoots. These findings provided a scientific basis for the management of bamboo forests and the enhancement of their economic benefits.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14122435/s1, Figure S1: Fresh yields of bamboo shoots without sheaths in different bamboo forest types. Different lowercase letters indicate significant differences between different bamboo forest types ($p < 0.05$); Figure S2: The linear mixed effect model of the effects of related factors on the nutritional (A protein content) and taste quality (B cellulose content; C lignin content) of bamboo shoots. (* for $p < 0.~05$, *** for $p < 0.001$). Notes: chl *a*: chlorophyll *a*; ca: carotenoid; ANPC: parenchyma cell number in the axial system; SL: scattered light; Figure S3: The linear mixed effect model of influencing factors and the parenchyma cell number in radial system (A), parenchyma cell diameter in radial system (B), parenchyma cell number in axial system (C) and parenchyma cell length in axial system (D) of bamboo shoot. (** for $p < 0.01$, *** for $p < 0.001$). Notes: chl *a*: chlorophyll *a*; ca: carotenoid.; Figure S4: The line mixed effect model of influencing factors on chlorophyll *a* (A) and carotenoid (B) contents in bamboo shoots. (* for $p < 0.~05$, *** for $p < 0.001$). Notes: CO: canopy openness; MLA: mean leaf angle; DL: direct light; SL: scattered light; Table S1: Coordinates, terrain, and canopy trees characteristics of sample collection of bamboo shoots plots (means ± SD).

Author Contributions: J.T. and C.S. designed the conceptual idea and the fieldwork; C.S., Y.Y. and M.W. collected the field data; W.L. conducted the random forest model and linear mixed effect analysis; C.S. analyzed the data and wrote the manuscript with input from J.T. and J.L. through multiple rounds of revision; A.A.A. polished the version of the manuscript. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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