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The relationship between growth, anatomical structure, and quality in different parts and stages of edible bamboo shoots of *Dendrocalamus latiflorus*

Lixin Huang[1†], Xiting Liao[1†], Daocheng Ma[1], Zailiu Li[1*] and Zhenguo Xu[2*]

Abstract

Background *Dendrocalamus latiflorus* is widely distributed in southern China and has high ornamental and edible value. The growth dynamics and the associations between growth and the distribution of nutrients or chemical components across various parts and stages of shoot development remain inadequately understood. In this study, tender shoots of *D. latiflorus* from Guangxi, China, were used to conduct experiments. During the edible growth period, the height, ground diameter, and morphology of the tender shoots were investigated, and the growth stages were classified by conducting ordered sample cluster analysis. The internal internode anatomy and nutritional/chemical components of the tender shoots at different growth stages and parts were measured and analyzed. The optimal harvesting stages and parts were determined by conducting a comprehensive analysis using the technique for order preference by similarity to the ideal solution (TOPSIS).

Results The height growth of *D. latiflorus* tender shoots lasted for 21 days and can be divided into four stages: I (0–9 d), II (10–13 d), III (14–17 d), and IV (18–21 d), while thickening growth lasted about 19 days. The moisture content of *D. latiflorus* tender shoots decreased as growth increased. Cell division and elongation increased the height of tender shoots. Among the four stages, cell division dominated in Stages I and II, whereas cell elongation dominated in Stages III and IV. The changes in nutrients and chemical components in different parts and stages of tender shoot development have distinct characteristics, and the differences are significant. The starch and reducing sugar contents reached a maximum value in the lower part of Stage II (10.19 $mg{\cdot}g^{-1}$, 18.87 $mg{\cdot}g^{-1}$), whereas the soluble sugar content reached a maximum value in the middle of Stage III (2.15 $mg{\cdot}g^{-1}$). The protein and fat contents were the highest in the upper part of Stage IV (3.84% and 4.8%). The contents of the chemical components of flavonoids and vitamin C were the highest in the middle of Stage IV (5.51 $mg{\cdot}g^{-1}$, 33.58 $mg{\cdot}100\ g^{-1}$), whereas the contents of cellulose and lignin in the later part of Stage IV were the highest (9.43% and 13.67%, respectively). Stage II (10–13 d) was the best harvest stage for *D. latiflorus* tender shoots, according to the comprehensive TOPSIS analysis, and the comprehensive quality of the upper part was the best in this stage. Additionally, the middle part of Stage III and the lower part of Stage IV were also high quality and could also be harvested.

[†]Lixin Huang and Xiting Liao contributed equally to this work.

*Correspondence:
Zailiu Li
lizailiu666@163.com
Zhenguo Xu
xuopingqing@126.com

Conclusions This study revealed the growth patterns of the tender shoots of *D. latiflorus* from morphological, anatomical, and physiological perspectives, as well as the dynamic changes in nutrient content during their growth. Within the 21-day edible stage, Stage II (10–13 days) was identified as the optimal harvesting stage, with the upper part of the shoot being the best section for harvest. This study provided a theoretical basis for further cultivating high-quality *D. latiflorus* for shoot production and has significant potential for increasing economic benefits.

Keywords *Dendrocalamus latiflorus*, Tender bamboo shoots, Growth rhythm, Anatomical structure, Nutrient/chemical component, Best harvest stages/parts

Introduction

Bamboo shoots refer to tender buds on the underground stem (bamboo whip or stalk base) of bamboo plants. Owing to its high taste and nutritional value, it is often treated as a vegetable. The whole shooting period (about 20–200 d) can be divided into different stages and shows a "slow-fast-slow" trend during this process. The growth rate, structure, nutrient, and chemical component contents differ among harvest times and parts, which depend on the species, biological characteristics, and growing conditions of the bamboo [39, 44, 60].

The rate of growth in length is different among various bamboo species. A large number of bamboo species (especially *Dendrocalamus* spp.) can reach tens of meters in size in a few months. For example, *D. hamiltonii* reaches a height of about 12 m after 105 days of rapid growth [22]. Similarly, *D. brandisii* and *D. latiflorus* need 82 days to reach a height of 7 m [29, 31]. However, some shrub-like bamboo (*Indocalamus* spp. and *Semiarundinaria densiflora*, among others) can reach a height of only 1–4 m after a transitory rapid growth period [63, 74]. Hence, there are many differences in vertical growth among various bamboo species. Additionally, the division and elongation of intercalary meristem cells (especially the longitudinal axis of the internode) determine the lengthening growth process [6, 71]. For the internode elongation of *Phyllostachys edulis*, cells divide first in the early stage, followed by elongation in the middle and late stages [17]. Moreover, the cell length increases from the upper part of the internode to the lower part, indicating basipetal progression [47]. Compared to the lengthening growth of bamboo shoots, the thickening growth of bamboo shoots is caused mainly by an increase in the cell volume and cell number of the pith meristem [14]. Owing to the lack of secondary growth in bamboo, thickening growth frequently completed before height growth [28, 69]. For example, the thickening growth of *D. farinosus* showed a "slow-fast-slow-stop" development trend, while thickening growth was completed in about 42 days [62]. To summarize, among the apical meristem types, the growth and development of the intercalary meristem determine the lengthening growth of bamboo shoots, whereas the pith meristem determines the thickening growth process.

The contents of inclusions, nutrient elements, and some secondary metabolites (such as lignin, flavonoids, and tannins) differ in various parts and growth periods of bamboo shoots and determine the flavor, nutritional value, and harvesting time during the whole growth period [45, 54]. In the early growth stage of bamboo shoots, sucrose is hydrolyzed generally into soluble sugars to provide energy to cells and perform basic respiration. Moreover, storage substances such as starch and fat accumulate progressively [35]. Starch hydrolyses as soluble sugar to provide energy during the rapid growth stage, whereas cellulose and lignin levels increase with cell elongation and thickening [47, 72]. Eventually, bamboo shoots become inedible due to lignification, the decomposition of nutrients, and a decrease in flavor. Additionally, nutrients and chemical components vary greatly among the bamboo shoot parts. For example, the protein content of *P. edulis* is lower in basal bamboo shoots than in tips, indicating a vertical distribution [27]. For *P. edulis* and *P. violascens*, the contents of protein, starch, fat, and vitamin C in bamboo shoot flesh are greater than those in bamboo shoot diaphragm [13]. The zinc content of *P. edulis* was considerably greater in the nodes with meristematic tissue than in the internodes, which might support rapid growth [50]. Therefore, selecting the best harvesting time and parts is critical for producing high-quality bamboo shoots.

Dendrocalamus latiflorus (family Gramineae/Bambusoideae) is a large sympodial bamboo that mainly inhabits the Guangxi Zhuang Autonomous Region, China. This bamboo thrives in warm environments, and Liuzhou City, known for its favorable climate, is one of the largest distribution areas for *D. latiflorus* in Guangxi. [26]. *Dendrocalamus latiflorus* can be used as ornamental bamboo in landscaping because of its luxuriant branches, and its tender shoots have a pleasant taste and high nutritional value (rich in protein, minerals, amino acids, and other substances). This species is one of the most important ingredients of Liuzhou River snail rice noodles (known as "Luosifen" in Chinese, with more than 50 billion yuan

worth of sales revenue per year for a complete industrial chain) [20]. The shooting period of *D. latiflorus* lasts for about 200 days, while the peak period extends from mid-July to early September (lasting for about 50 days). However, the moisture content of *D. latiflorus* shoots decreases gradually and becomes fibrotic with rapid growth, resulting in low edible availability. Therefore, the differences in nutrient and chemical component contents among different growing stages and parts of *D. latiflorus* shoots need to be determined to support the Liuzhou River snail rice noodle industry in China and worldwide. Some studies have shown that *D. latiflorus* shoot height can rapidly increase to 13 m during the height growth period (90 days). This period can be divided into a tender shoot sprouting period, a germination period, a growth period, and a rapid growth period [75]. The shoots in the growth period have the highest quality (higher carbohydrate content and lower cellulose content) [29, 31]. However, in the above studies, the researchers only observed and recorded the morphological changes in *D. latiflorus* from the tender shoot to the young bamboo, without investigating the anatomical structure and the correlation between lengthening and thickening growth. Additionally, the growth periods were vaguely defined, which made it impossible to determine the duration of the edible period of the tender shoots. Additionally, the differences in nutrient and chemical component contents among different parts have not been determined, and nutrient accumulation effects during growth and development need to be thoroughly investigated.

Based on previous studies, the growth rhythm, morphology, and internal internode anatomy of tender shoots of *D. latiflorus* were investigated in this study. Additionally, the differences in nutritional and chemical components among different growth stages and parts of tender shoots were analyzed. We hypothesized that (i) the growth and development of tender bamboo shoots are related to an increase in cell number and size; cells first become more numerous and then larger. (ii) With the growth and development of the tender shoots of *D. latiflorus*, the moisture and sugar contents gradually decreased, whereas fat, dietary fiber, flavonoids, and vitamin C gradually accumulated. (iii) The middle growth period of tender shoots is the best harvesting period, and the upper and middle parts of tender shoots are the best edible parts. In this study, we analyzed and solved the following scientific questions: (i) What are the rhythms of lengthening and thickening of *D. latiflorus* tender shoots? How long is the edible period of the tender bamboo shoots? (ii) What are the changes in nutrient and chemical components of *D. latiflorus* tender shoots during the growth process? What is the best stage and part for harvesting and eating? We aimed to establish a theoretical framework that facilitates the comprehension of bamboo shoot growth dynamics and nutrient changes, advances industrial standardization, and contributes to the Liuzhou River snail rice noodle industry.

Materials and methods

Experimental setting area

The study was conducted at the bamboo shoot planting base (24.402°N, 109.605°E) in Luorong Town, Liuzhou City, Guangxi Zhuang Autonomous Region, which has a subtropical monsoon climate (with an average annual temperature of 20 °C, average annual precipitation of 1252.7 mm, rainfall concentrated from April to August every year, 180 days of annual sunshine, and a frost-free period of 300 days). The area of the bamboo shoot planting base is 53 hm^2, which is suitable for the growth of *D. latiflorus* tender shoots (Figure S1). The seedlings used at the base were one-year-old main branch cuttings seedlings. The main branches were collected in March 2002 from *D. latiflorus* base in Qingyuan, Guangdong Province. After rooting through cutting and a hardening-off process, seedlings with good growth and a height of 60–70 cm were selected for afforestation. The forest land consisted of neutral soil with a thickness of approximately 1 m and a slope of 45°. After land preparation, the seedlings were planted at a spacing of 6 m × 4 m. Each planting pit (60 cm × 60 cm × 50 cm) was amended with 7–8 kg of organic fertilizer to promote initial growth. After the bamboo forest was established, compound fertilizer (N:P:K = 22%:8%:15%) was applied once a year in late April, with a single application rate of 4 kg per clump.

Plant materials

After *D. latiflorus* was identified by Associate Professor Zailiu Li (Guangxi University), nine 20 m × 20 m plots were randomly established at the study sites, as described in Sect. "Experimental setting area" [75]. From each sample plot, 15 shoots with robust development, favorable growth, and no pests or diseases were selected and numbered. The growth regularity data of the tender bamboo shoots were collected from the date they were unearthed (July 1, 2022, which indicated a height of 2–5 cm) until they underwent lignification and became inedible (July 22, 2022). Ordered sample clustering analysis was performed to partition the acquired data into distinct growth stages, after which the samples were collected within each stage (starting from July 23, 2022). In total, 27 tender bamboo shoots were collected at each time point, with three shoots from each plot being healthy. After removing the soil, the tender shoots were divided into three equal lengths based on the length of the edible part (which remained after the shoot sheaths and the shoot stump

were removed). The edible portions were designated the upper part, the middle part, and the lower part, respectively (Figure S2-A ~ B). The samples were transported to the laboratory on dry ice and stored at −4 °C for determining nutrients.

Index determination

Shoot growth status

The growth indices were measured every day from July 1st to 22nd. The height was measured with steel tape to within 0.01 cm (from the unearthed surface to the top end of the bamboo shoot body), and the ground diameter was measured using digital Vernier calipers to within 0.01 mm (the unearthed surface of the bamboo shoot body).

Anatomical structure

The paraffin sections were prepared following the protocol provided by Li [25]. Bamboo shoot samples were categorized into combinations of 4 developmental stages (I–IV) and 3 distinct parts (upper, middle, and lower internode), resulting in 12 unique group. For each group, both transverse and longitudinal sections were prepared, with 3 biological replicates per section type. In total, this resulted in 72 section preparations. A 10 g sample of each part was cut into 1 cm^3 pieces, placed in FAA fixing solution (70% alcohol:glacial acetic acid:formalin = 90:5:5) (v/v/v), sealed with a rubber stopper and tape, and transported to the laboratory for storage at 4 °C for anatomical observation (Figure S2-D). The samples were soaked in FAA fixative solution and dehydrated with 70%, 80%, 85%, 95%, or 100% alcohol for 1 h each. Transparent treatment was then performed using a mixture of half anhydrous alcohol and half xylene (v/v), followed by pure xylene, for 1 h each. The material was impregnated in 50% xylene and 50% low-melting paraffin wax at 56–58 °C for 12 h, followed by 8 h in high-melting wax at 60–62 °C. The sample was embedded at 64 °C, cooled, and solidified for later use. A microtome (Leica RM 2245, Germany) was used to slice the samples, with 6 slices prepared per biological replicate. After the samples were dewaxed, they were dyed and sealed. Finally, observations were made, and photographs were captured using a microscope (Zeiss Axio ImagerZ2, Germany). Structures were selected based on their representativeness and uniformity, with a focus on specific features such as vascular bundles and parenchyma cells. A minimum of 6 fields of view were analyzed per sample to ensure robust and statistically reliable data.

Moisture content

The drying method was used to determine the upper, middle, and lower moisture contents of tender shoots at different stages [36] (National Health and Family Planning Commission of the People's Republic of China, 2016). The fresh sample and then the dried sample were weighed again to measure the moisture content (the samples were placed in a blast drying oven at 105 °C for 15 min and then dried at 70 °C to a constant weight). Moisture content = (fresh weight of sample—dry weight of sample)/fresh weight of sample × 100%.

Nutrients and chemical components

Nutrients and chemical components were determined following the protocols developed by Gao et al. [15] and Wu [59].

Lignin content The acid hydrolysis method was used to determine lignin content. The samples were placed in a blast drying oven at 105 °C for 15 min, dried at 70 °C to a constant weight, crushed through a 60-mesh screen, and then placed in a dryer for use. The dry sample was extracted for 24 h with deionized water. After drying, it was treated with 72% concentrated sulfuric acid (0.3 g sample/3 mL acid), diluted to 4% with deionized water, and hydrolyzed in a steam pressure cooker. The hydrolysate was filtered and dried to make lignin.

Flavonoid content The sodium nitrite-aluminum nitrate colorimetric method and a standard curve were used to determine the flavonoid content. First, one gram of sample was placed in a Soxhlet extractor, 100 mL of 70% ethanol, and a small amount of $CaCO_3$ was added. The sample was extracted for 6–8 h and concentrated under reduced pressure. The concentrated liquid was washed with ethyl ether and then diluted to a final volume of 100 mL with 70% ethanol to prepare the sample solution. After absorbing 1 mL of sample solution, 1 mL of 70% ethanol, 0.3 mL of 5% $NaNO_2$, 0.3 mL of 10% $Al(NO_3)_3$, and 2 mL of 4% NaOH were added every 6 min to examine the mixed solution. After 10 min, a spectrophotometer was used to measure the absorbance at 510 nm. A standard solution of 100 $\mu g \cdot mL^{-1}$ was prepared with rutin and 70% ethanol, followed by dilution to a working concentration of 0–50 $\mu g \cdot mL^{-1}$. The INFINITE M200 PRO instrument (Tecan, Maunnedorf, Switzerland) was used for color comparison.

Soluble sugar and starch contents The anthrone colorimetric method and standard curve were used to determine the contents of soluble sugar and starch. Briefly, 20 mg of sample was added to 10 mL of distilled water and extracted in an 80 °C water bath for 60 min. After 40

mg of activated carbon was added and decolorized at 80 °C for 30 min, it was removed and cooled to room temperature. To determine the soluble sugar content, 1 mL of filtrate was removed, 10 mL of anthranone reagent was added, and the mixture was incubated at 90 °C for 15 min. After cooling to room temperature, the absorbance was measured at 625 nm. After the precipitate was dissolved in a small amount of iodine solution, anthrone was added, and the mixture was heated in a water bath and cooled to room temperature. To measure the starch content, the absorbance was measured at 625 nm. A standard solution of 100 μg·mL^{-1} was prepared with sucrose and deionized water and then diluted to a working concentration of 0–100 μg·mL^{-1}. The INFINITE M200 PRO instrument was used for color comparison.

Reducing sugar content The 3,5-dinitrosalicylic acid (DNS) method and a standard curve were used to determine the content of reducing sugars. First, 2 mL of the sample was mixed with 2 mL of DNS reagent, and the color was developed in a water bath at 90 °C for 6 min before cooling to room temperature. After diluting the samples to 25 mL with water, the absorbance was measured at 540 nm. A standard solution (1 mg·mL^{-1}) was prepared with pure glucose and deionized water and then diluted to a working solution of 0–1 mg·mL^{-1}. The INFINITE M200 PRO instrument was used for color comparison.

Cellulose content The anthrone-H_2SO_4 method and a standard curve were used to determine the cellulose content. The samples were placed in a cold bath with 60% H_2SO_4 and 100 mg samples for 30 min. After filtration, 2 mL of the filtrate was diluted. Next, 0.5 mL of 2% anthranone reagent and 5 mL of concentrated H_2SO_4 were added, and the absorbance was measured at 620 nm. A 100 μg·mL^{-1} standard solution was prepared using pure cellulose and 60% H_2SO_4 and then diluted with deionized water to obtain a working solution with a concentration of 0–100 μg·mL^{-1}. The INFINITE M200 PRO instrument was used for color comparison.

Vitamin C content The 2,6-dichlorophenol indophenol titration method was used to determine vitamin C content. A slurry was made from a suitable sample in 2% oxalic acid. The sample was stirred and filtered in a volumetric flask, and the homogenate was diluted. The sample was titrated with 2,6-dichlorophenol indophenol until the filtrate turned pink and was stable for 15 s.

Protein content The Coomassie brilliant blue method and a standard curve were used to determine the protein content. First, one gram of pulverized homogenate was washed in a 100-mL volumetric flask with 80 mL of water, and ultrasonicated for 15 min. After centrifugation at 4,000 r/min for 15 min, 0.5 mL of the supernatant was aspirated, and 0.5 mL of distilled water and 5 mL of Coomassie Brilliant blue G-250 solution were added. The mixture was shaken and left undisturbed for 2 min. The absorbance was measured at 595 nm. A standard solution of 0.1 mg·mL^{-1} was prepared using bovine serum albumin and deionized water and then diluted to a working concentration of 0–0.1 mg·mL^{-1}. The INFINITE M200 PRO instrument was used for color comparison.

Fat content The cable extraction method was used to determine the fat content. Anhydrous ether was injected to fully immerse the filter paper package after the sample was wrapped in it and placed in the extraction cylinder. The filter paper package was removed after extraction. The ether was volatilized in the ventilation area, and the filter paper package was dried in a 105 °C oven until a constant weight was reached.

Data analysis

Microsoft Excel 2018 was used to statistically analyze the data and ordered sample cluster analysis [46] was performed to classify different stages of height growth. IBM SPSS 26.0 statistical software (IBM Corp., Armonk, NY, USA) was used for two-factor analysis of variance (significance test at $P=0.05$ level). Duncan's method was used for multiple comparisons, and Origin 2022 was used to plot graphs. The best time and part of shoot harvesting were evaluated using the TOPSIS comprehensive evaluation method [70].

Results

Growth and moisture content

The height growth of the edible tender bamboo shoots of *D. latiflorus* lasted for 21 days. The color of the shoot sheaths became progressively deeper, whereby the upper part transformed from a pale green hue to a yellow-green hue, while the base gradually turned brown (Fig. 1-A-I ~ IV). Eventually, the inner part of the shoots turned green from white and became inedible due to lignification. Based on the results of ordered sample clustering, this stage was divided into four stages. The average daily height gains for Stages I (0–9 d), II (10–13 d), III (14–17 d), and IV (18–21 d) were as follows: 1.77 cm, 4.32 cm, 6.63 cm, and 11.48 cm, respectively. The average daily increase in thickening was 0.32 cm, 0.35 cm, 0.32 cm, and 0.13 cm, respectively. By considering the height growth time as the independent variable and the height of tender bamboo shoots during various stages as the dependent variable, the height growth equation was derived as follows: $Y=0.0091\ x^3—0.009\ x^2+1.1199\ x+2.8949$

(Fig. 1-B). By considering the thickening growth time as the independent variable and the average ground diameter of tender bamboo shoots during various stages as the dependent variable, the thickening growth model of the logistic function was obtained ($R^2 = 0.991$) (Fig. 1-C). The lengthening and thickening of the bamboo shoots were correlated nonlinearly with the growth stage. To summarize, the height growth of *D. latiflorus* tender shoots lasted 21 days, indicating a slow-fast trend. The ground diameter remained constant at about 19 d, exhibiting "slow-fast-slow" characteristics, and the thickening growth stopped before the lengthening growth.

Extremely significant differences were recorded in moisture content among different parts of tender shoots in Stages I, II, and IV ($P < 0.01$), whereas significant differences were recorded in Stage III ($P < 0.05$) (Table S2). The moisture content decreased gradually with growth, and the order was always the upper part > middle part > lower part (Fig. 1-D). Among them, the moisture content reached its maximum in the upper part of Stage I (93.32%), and the moisture content in the lower part of Stage IV was the lowest (78.34%) (Table S1). Generally, the moisture in the tender shoots decreased gradually, and the moisture content in the upper part of the shoot was the highest during the same stage.

Anatomical structure observation

In Stage I, the upper, middle, and lower internode parenchyma cells divided rapidly. The vascular bundles in the middle and lower internodes first appeared (Figs. 2-I-A ~ C and 3- I-A ~ C); internode cell length and fiber cell number increased gradually during Stages II ~ III, whereas upper internode parenchyma cells continued dividing rapidly. However, the nuclei of certain parenchyma cells in the middle and lower internodes were difficult to discern, indicating that their cellular division ceased. Additionally, the inner diameters of vascular bundles, including annular vessels and pitted vessels, progressively enlarged and became mature (Figs. 2-II-A ~ C, III-A ~ C and 3-II-A ~ C, III-A ~ C), the upper internode cells continued dividing rapidly during Stage IV, whereas the cells of the middle and lower internodes differentiated fully, the parenchyma cells were tightly packed, and the vascular bundle matured further. Simultaneously, the mean length of the cells remained unchanged, indicating the end of cell elongation (Figs. 2-IV-A ~ C and 3-IV-A ~ C).

Nutrient and chemical contents

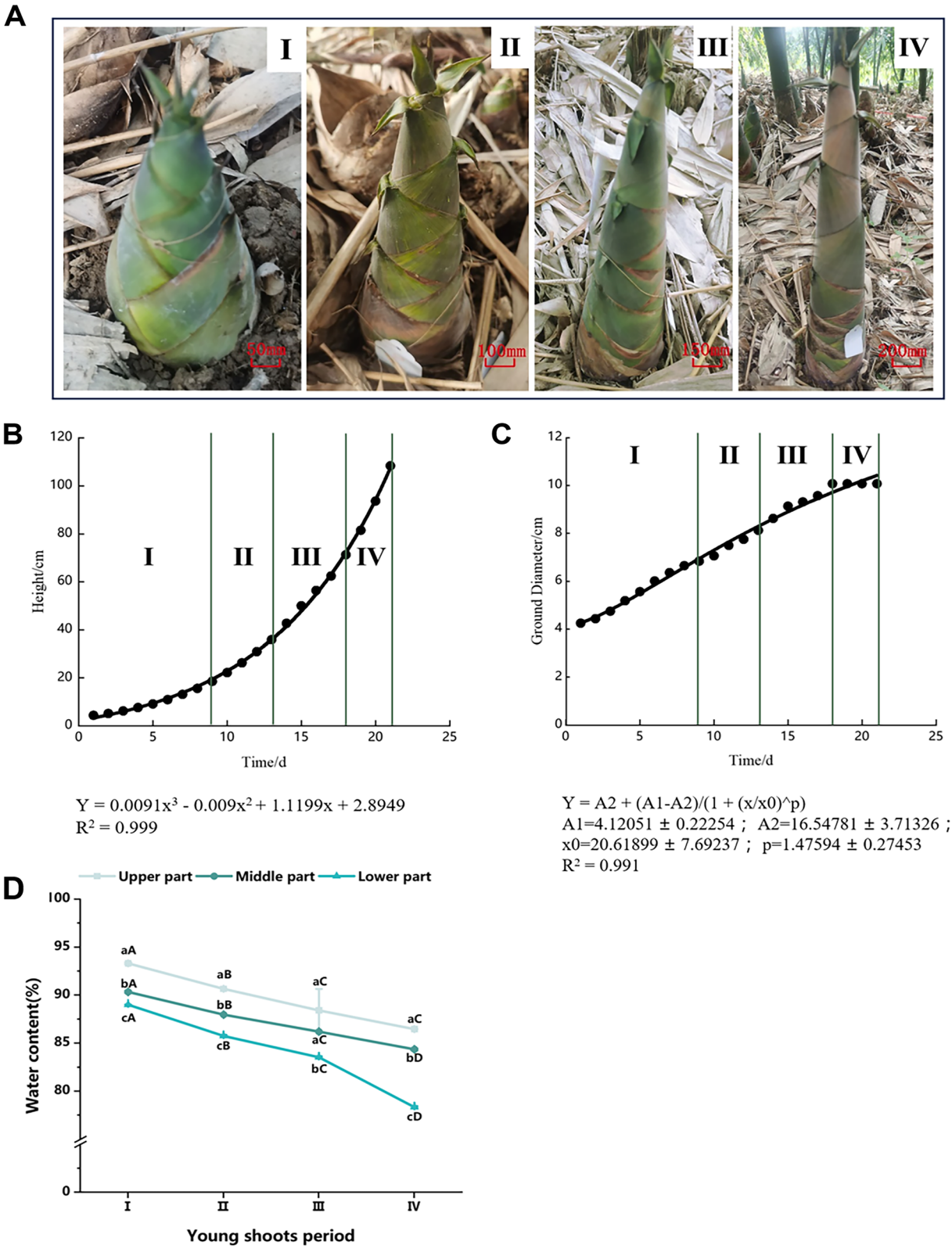
Except for the content of soluble sugars in different parts of Stage I ($P < 0.05$), the contents of nutrients and chemical components in the same part at different stages and between different parts of tender bamboo shoots were extremely significant ($P < 0.01$) (Table S3 ~ S11). The starch and reducing sugar contents reached a maximum value in the lower part of Stage II (10.19 $mg \cdot g^{-1}$, 18.87 $mg \cdot g^{-1}$), whereas the soluble sugar content reached a maximum value in the middle of Stage III (2.15 $mg \cdot g^{-1}$). The protein and fat contents were the highest in the upper part of Stage IV (3.84% and 4.8%, respectively). The contents of the chemical components of flavonoids and vitamin C were the highest in the middle of Stage IV (5.51 $mg \cdot g^{-1}$, 33.58 $mg \cdot 100\ g^{-1}$), whereas the contents of cellulose and lignin in the later part of Stage IV were the highest (9.43% and 13.67%, respectively) (Table S1). Generally, with the growth of tender shoots, the protein content first decreased and then increased in the upper and lower parts but increased gradually in the middle part (Fig. 4-A). The starch content first increased and then decreased in all three parts (Fig. 4-B). The fat content increased in the upper and middle parts but showed an "up-down-up" trend in the lower parts (Fig. 4-C). The content of reducing sugars showed an "up-down-up" trend in all parts (Fig. 4-D). The soluble sugar content showed an "up-down-up" trend in the upper and lower parts but a "down-up-down" trend in the middle (Fig. 4-E). The contents of flavonoids, cellulose, vitamin C, and lignin increased in all samples (Fig. 4-F ~ I). The changes in nutrients and chemical components in different parts and stages of tender shoot development have distinct characteristics, and the differences are significant.

Comprehensive assessment

The TOPSIS comprehensive evaluation method revealed that Stage II had the highest main nutrient scores; this indicated that Stage II was the optimal bamboo shoot harvesting stage (Table 1). Tender bamboo shoots located in the upper part of Stage II, the middle part of Stage III,

(See figure on next page.)

Fig. 1 External morphological changes in tender shoots at different times. **A** Tender shoots in stages I, II, III, and IV; **B** Height growth model of tender bamboo shoots of *D. latiflorus*;**C** Ground diameter growth model of tender bamboo shoots of *D. latiflorus*; **D** Changes in moisture content in different parts of tender bamboo shoots during different stages. Note: Different lowercase letters indicate a significant difference in moisture content among different parts during the same stage ($P < 0.05$). Different capital letters indicate a significant difference in the moisture content of the same part between different stages ($P < 0.05$)



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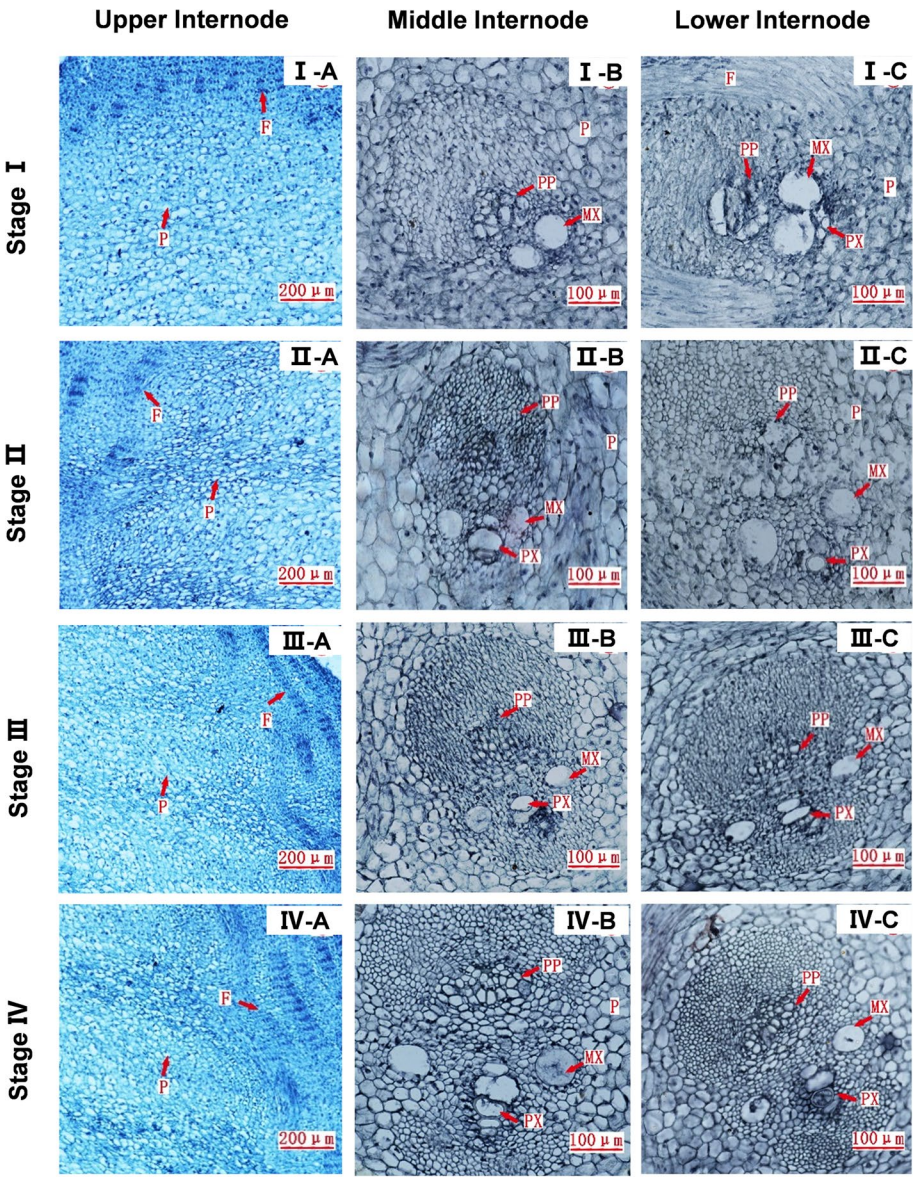

Fig. 2 Observation of the anatomical structure of the intersegmental cross-sections of the tender bamboo shoots from different stages and different parts. (Note: I, II, III, and IV are stages I, II, III, and IV, respectively; **A**, **B**, and **C** are the upper, middle, and lower internodes, respectively; P: Parenchymal cells; F: fibroblasts; PX: native xylem; PP: native phloem; MX: pitted vessel.)

and the lower part of Stage IV received higher scores and were the best edible parts.

Discussion

Growth rhythm and moisture content changes in *D. latiflorus*

Various factors affect the process of lengthening and thickening growth, including plant characteristics and ecological conditions. The height growth of *D. latiflorus* tender shoots lasted for 21 days, indicating the trend of "slow-fast", which was consistent with the observation of bamboo shoots of *P. edulis*, *Bonia amplexicaulis*, and *D. sinicus* in their early growth [6, 30, 37]. After 19 days of breaking through the soil, the thickening growth tended to stop. Similarly, the thickening growth of *P. edulis* tender shoots started slowing down about 15 days after unearthing and eventually stopped about 25 days later. The entire growth cycle finished before the completion of height growth [8]. Additionally, environmental factors can significantly affect growth status. For example, Zhou [75] found that the primary meteorological factors affecting the daily height growth of *D. latiflorus* were

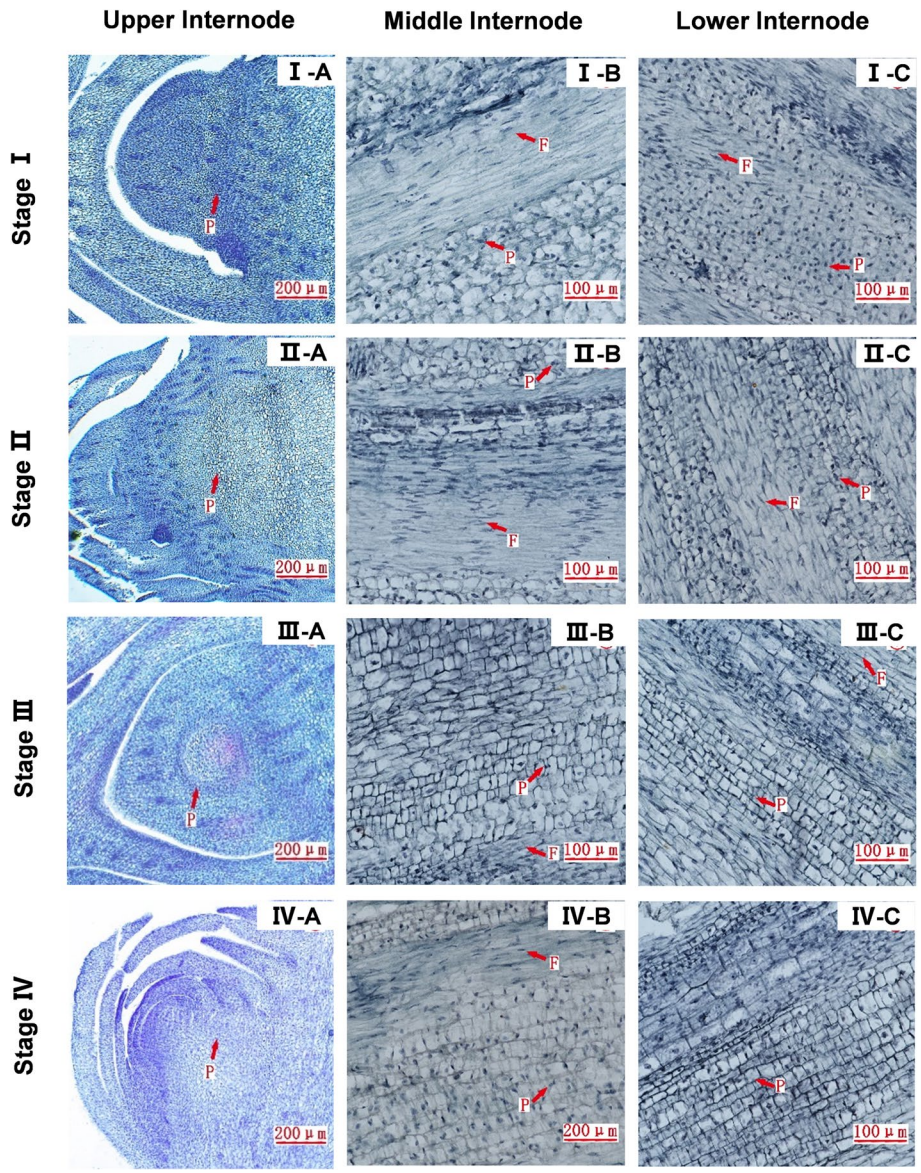

Fig. 3 Observation of the longitudinal section anatomy of the internode of the tender bamboo shoots in different stages and different parts. (Note: I, II, III, and IV are stages I, II, III, and IV, respectively; **A**, **B**, and **C** are the upper, middle, and lower internodes, respectively; P: Parenchymal cells; F: fibroblasts; PX: native xylem; PP: native phloem; MX: pitted vessel.)

sunshine duration, the previous day's temperature, the previous day's rainfall, and the current day's minimum temperature. Additionally, the diurnal patterns of light intensity and temperature were largely consistent with the rhythmic changes in the daily height growth of *D. latiflorus*. Given the limitation of this study in not explicitly investigating the effects of environmental factors on shoot growth, this insight provides valuable guidance for our future research directions. To summarize, the species and biological characteristics of bamboo shoots primarily determine their growth and development, and environmental factors can alter the initial growth rhythm by influencing their growth status. Additionally, each internode in bamboo shoots is the fundamental unit of rapid growth, and different internodes exhibit a developmental gradient [58]. Therefore, investigating individual internodes to further assess their growth rhythm, not limited to the morphology of the entire bamboo shoot, is necessary.

This study also revealed that the moisture content of *D. latiflorus* tender shoots reached its maximum in the upper part of Stage I and decreased as growth increased.

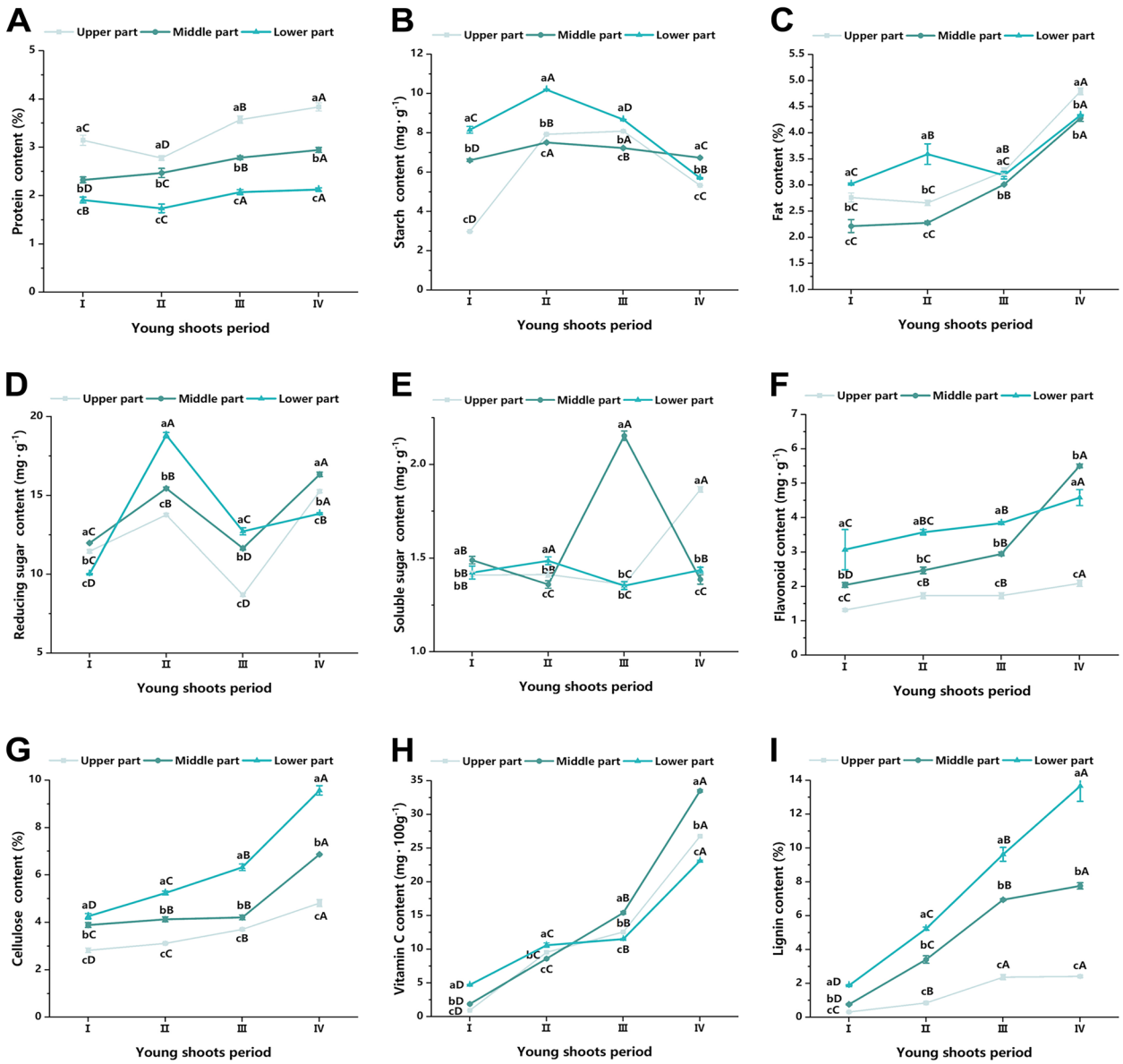

Fig. 4 Changes in nutrient contents in different parts of tender bamboo shoots during different stages. Note: Different lowercase letters indicate significant differences in nutrient contents among different parts during the same stage ($P < 0.05$). Different capital letters indicate significant differences in the nutrient content of the same part between different stages ($P < 0.05$)

Similarly, the moisture content of *C. tumidissinoda* decreased from 91.66% to 90.26% as the height of the bamboo shoots increased to 30 cm [68]. This change can be attributed to various physiological processes that consistently consume water, including respiration and transpiration. Moreover, studies have shown that water is associated with the growth of plant cells and that cell elongation is achieved by changing cell wall properties and turgor pressure [3]. In this study, the moisture content of tender shoots consistently showed a gradient difference from the upper to the lower parts, which was consistent with the results of bamboo shoots of *C. utilis* [40]; this could be attributed to the growth status and maturity of different internode cells. Dünser et al. [12] reported significant differences in vacuole occupancy between meristem cells and elongated zone cells, but the mechanism behind this phenomenon needs to be elucidated. Additionally, the moisture contents of the middle and upper parts of Stage I and the upper parts of Stages II and III exceeded 90%, which were found to be more tender [51].

Table 1 TOPSIS comprehensive evaluation ranking of tender bamboo shoots of *D. latiflorus* at different stages and parts

Variate		Positive ideal solution distance (D+)	Negative ideal solution distance (D-)	Composite score index	Sort
Stage	Stage II	0.539	0.71	0.568	1
	Stage III	0.614	0.597	0.493	2
	Stage IV	0.691	0.64	0.481	3
	Stage I	0.747	0.564	0.430	4
Stage and part	Middle part of Stage III	10.464	34.313	0.766	1
	Upper part of Stage II	11.663	28.221	0.708	2
	Lower part of Stage IV	19.789	22.931	0.537	3
	Upper part of Stage III	21.383	17.229	0.446	4
	Lower part of Stage I	24.013	17.080	0.416	5
	Upper part of Stage IV	24.550	17.416	0.415	6
	Middle part of Stage I	24.961	16.669	0.400	7
	Lower part of Stage II	26.210	14.697	0.359	8
	Middle part of Stage IV	25.292	13.662	0.351	9
	Upper part of Stage I	34.300	15.534	0.312	10
	Lower part of Stage III	30.721	12.493	0.289	11
	Middle part of Stage II	32.920	13.092	0.285	12

According to the Technical Regulations for the Production of Bamboo Shoots for River Snails Rice Noodle Raw Materials in Liuzhou (DB4502/T 0002–2022), tender shoots in Stage III meet Grade I (unearthed length 40–50 cm) or Grade II (unearthed length 50–60 cm) standards, whereas tender shoots in Stage IV meet Grade III (unearthed length ≥ 60 cm) standards. Based solely on the appearance of bamboo shoots, Stage III represents the optimal time to harvest tender shoots. However, based on the comprehensive evaluation of nutritional value and taste, Stage II scored the highest according to the TOPSIS method, which was the optimal time to harvest bamboo shoots of *D. latiflorus*, and the upper part was the best in this stage. Among the other stages and parts, the middle part of Stage III and the lower part of Stage IV obtained higher scores, indicating superior quality.

Morphological characteristics of the internode cells of tender shoots

The internode elongation of tender shoots is related to cell division and elongation of the intercalary meristem [61]. This study revealed that cell division primarily influences the elongation of internodes during Stages I and II, whereas cellular elongation serves as the determining factor during Stages III and IV. Rapid cell elongation manifests as rapid internode growth, resulting in a "slow-fast" trend in the height growth of *D. latiflorus*. Similarly, Dong [11] reported that the early internode growth of *Phyllostachys varioauriculata* was dominated by cell division and cell elongation, whereas it later transitioned to cell elongation. The dynamic changes in cell length and nuclear number indicate cell elongation and division [10]. In this study, the upper internode cells consistently exhibited robust division, characterized by abundant cytoplasm and large nuclei. In contrast, the middle and lower internode cells started elongating in Stage II, while the meristem area decreased over time, and the ability of cells to divide weakened, which agreed with the observations in *P. edulis* [21]. The differentiated vascular bundles matured. No significant difference was recorded in average cell length until cell differentiation was complete, indicating the end of cell elongation. Dong [11] reported that the internode elongation of *P. varioauriculata* is basipetal. The findings of this study showed that the fundamental structure of the internode is composed of vascular bundles distributed in parenchyma cells, which are similar to those of *P. edulis* [64], *D. farinosus*, *D. asper*, *B. pervariabilis*, and other bamboo species [7]. However, studies on internode elongation have rarely focused on vascular molecules because of their complicated structure. Luo et al. [33] found no significant difference in the width of vessel elements among four species of sympodial bamboo, but the morphological characteristics differed. Further studies are needed to determine whether *D. latiflorus*, also known as sympodial bamboo, possesses this characteristic. Moreover, with the innovation of various sequencing technologies, studies on the molecular mechanism of rapid bamboo growth, such as transcriptome studies [6, 58], genome-wide analysis of circular RNA [56], DNA methylation analysis [23, 37], and GA-related gene subgenomic analysis [34], have been performed. However, owing to its polyploidy and large

genome size, the genome sequence of *D. latiflorus* was not reported until Zheng et al. [73] provided high-quality hexaploid genome data.

Study of nutrient accumulation in tender bamboo shoots

The content, transportation, utilization, and storage of sugars in plant cells are influenced by environmental factors, cell physiological activities, plant development stage, and other factors [19]. The starch content of *Phyllostachys prominens* increases during the early growth stage of tender bamboo shoots [41], which was also found in this study. After tender bamboo shoots emerge from the ground, photosynthesis intensifies, and starch accumulates as a storage substance. During Stages III and IV, starch is degraded through enzymatic reactions to provide energy for the rapid expansion of internode cells, resulting in a decrease in content [76]. The results indicated that the contents of reducing sugars and soluble sugars exhibited an "up-down-up" trend. This can be attributed to the fact that the hydrolysis of sucrose led to an initial increase in Stages I and II, which were subsequently used to supply energy for rapid growth in Stages III and IV. Non-structural carbohydrates can be transferred from mature stems to tender shoots through underground rhizomes during rapid growth to provide enough energy for their growth [43]. This transfer mechanism is a reason for the increase in reducing sugar and soluble sugar contents in tender shoots. Additionally, the sweetness of bamboo shoots mainly depends on the content of soluble sugars. The highest soluble sugar content was found in the middle part of Stage III in this study, indicating that tender bamboo shoots have a superior flavor.

Protein, as a critical constituent of plant cells, participates in physiological processes, including cell division and elongation. The results indicated that the protein content increased with the growth of tender shoots. Many proteins are synthesized to maintain cell morphology, facilitate material transportation, enable signal transduction, and perform other essential functions [1, 48]. A large amount of nitrogen is absorbed from the soil and used as a supplement to the raw material for protein synthesis. Additionally, protein synthesis activity is significantly greater in the upper parts of the bamboo shoots than in the other parts because of the consistently vigorous cell division, which results in greater protein content in the former than in the latter; this finding is consistent with the findings of Lin et al. [27]. In this study, the protein content in the upper part of tender bamboo shoots in Stages III and IV was high, and appropriate consumption can supplement protein.

The results showed that the fat content increased with the growth of tender shoots. Similarly, Wang et al. [55] reported that the total fat content increased significantly compared to that of new bamboo shoots after 10 days of growth. Fat accumulates as a storage substance. Low fat content is one of the characteristics of bamboo shoots (fat content ≤ 3 g per 100 g of solid), thus it is considered to be a healthy food for overweight, diabetic, or hyperlipidemic patients [9].

The results showed that the contents of cellulose and lignin increased with the growth of tender shoots, which was consistent with the findings for the bamboo shoots of *D. asper*, *D. strictus*, *Bambusa tulda*, and *P. edulis* [38, 65]. This trend can be attributed to vigorous cell division and elongation activities because cellulose and lignin are the main components of the cell wall [53]. Additionally, the content in the lower part was significantly greater than that in the middle and upper parts because the cells in the middle and lower parts lignify and differentiate first. The Chinese Nutrition Society and the EFSA both advise that individuals consume 25 g of natural dietary fiber daily from food sources. The lignin content of tender shoots at Stages III and IV was high, and appropriate consumption could supplement dietary fiber. Moreover, the increase in lignin content results in the hardening of tender shoots, which decreases their taste and edible value [18]. Therefore, Stages I and II are more tender and refreshing.

The findings of this study revealed that the flavonoid content progressively increased in all parts with tender shoots, with the upper part consistently exhibiting a significantly lower flavonoid content than the middle and lower parts. Similarly, *C. tumidissinoda* exhibited a similar pattern [52], and the flavonoid contents of *Bambusa oldhami* and *P. edulis* increased from the upper parts to the lower parts of the shoots [24]. Besides structural genes and transcription factors, complex environmental elements (light, temperature, soil conditions, etc.) influence the synthesis and metabolism of flavonoids in plants [16, 57, 67]. For example, prolonged exposure to sunlight can increase the content of flavonoids to protect plants against light erosion [49], and high temperatures also promote the production of secondary metabolites [66]. Therefore, the increase in flavonoid content may be attributed to an increase in light time and ambient temperature following the unearthing of bamboo shoots, but the mechanism underlying this increase in flavonoid content in bamboo shoots needs to be elucidated. Flavonoids, which are significant secondary metabolites found in plants, possess antioxidant, anti-inflammatory, and enzyme activity-regulating properties [5]. However, the bitter flavor of flavonoids imparts bitterness to various foods [42]. Therefore, with the growth of tender bamboo shoots, their palatability decreases, which is consistent with the results of studies on other bamboo shoots

reported by Bhardwaj et al. [2] and Lin et al. [27]. To summarize, the upper and middle parts of Stages II and III presented a superior quality of tender bamboo shoots.

The content of vitamin C in all parts gradually increased, similar to that found in *P. prominens* [41]. Constant light treatment increases the vitamin C content of *Vigna radiata* beyond its initial concentration. Additionally, light can regulate the gene expression patterns associated with vitamin C biosynthesis and regeneration [32]. Therefore, one of the reasons for the increase in vitamin C content is prolonged exposure to light after shooting. The Chinese Nutrition Society recommends that each person consume 100 mg of vitamin C per day, whereas the EFSA recommends 95–110 mg. Since many staple foods, such as cereals, contribute little to dietary vitamin C intake, fresh vegetables and fruits serve as the primary sources of this nutrient in daily diets. The vitamin C content reaches its peak of 33.58 mg·100 g^{-1} in the middle part of Stage IV, which is even comparable to some vegetables with high vitamin C content, such as spinach [4]. Therefore, consuming bamboo shoots at this stage can significantly contribute to meeting the daily vitamin C requirements of the human body and effectively help prevent scurvy.

In summary, this study offers valuable insights into the early growth and metabolism of *D. latiflorus* tender shoots. However, it is equally important to acknowledge the limitations in the depth of our investigation. The molecular mechanisms underlying the key findings of this study remain unclear. Future research will focus on constructing a molecular regulatory model for the growth and metabolism of *D. latiflorus* tender shoots by employing multi-omics technologies, thereby providing a theoretical basis for the precise regulation of edible bamboo shoot quality.

Conclusion

This study revealed the growth patterns of the tender shoots of *D. latiflorus* from morphological, anatomical, and physiological perspectives, as well as the dynamic changes in nutrient content during their growth. The height growth of *D. latiflorus* tender shoots lasted for 21 days and could be divided into four stages: I (0–9 d), II (10–13 d), III (14–17 d), and IV (18–21 d), whereas the thickening growth lasted about 19 d. Among the four stages, cell division dominated in Stages I and II, whereas cell elongation dominated in Stages III and IV. The changes in nutrients and chemical components in different parts and stages of tender shoot development have distinct characteristics, and the differences are significant. Stage II (10–13 d) was the best harvest stage for the tender shoots of *D. latiflorus*, and the comprehensive quality of the upper part was the best in this stage. This study provided a theoretical basis for further cultivation of high-quality *D. latiflorus* for shoot production and has significant potential for increasing economic benefits. Future research will focus on the molecular mechanisms and environmental influences regulating the growth and metabolism of *D. latiflorus* tender shoots to optimize cultivation and enhance yield and quality.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12870-025-06294-3.

Supplementary Material 1: Figure S1. Experimental location and introduction of Liuzhou River snail rice noodles. Figure S2. Material handling. Table S1. Nutrient content of tender shoots in different stages and different parts. Table S2-S11. F-values and P-values of nutrient/chemical component contents.

Authors' contributions

L. H. contributed to the writing of the original draft, provided visualization, conducted investigations, and performed formal analysis. X. L. was involved in investigation and formal analysis. D. M.contributed to writing by reviewing and editing the manuscript. Z. L. was responsible for conceptualization, supervision, providing resources, project administration, and funding acquisition. Z. X. contributed resources and acquired funding. All authors read and approved the final manuscript.

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Data availability

The datasets used during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

This manuscript does not involve researching about humans or animals. The plant samples used in this study were cultivated artificially and are not listed in the CITES Appendices (Convention on International Trade in Endangered Species of Wild Fauna and Flora). The study was carried out in accordance with Chinese laws, international guidelines, and local regulations, and was approved by the base management. The samples were formally identified by Associate Professor Zailiu Li (Guangxi University). Voucher specimens are scientifically deposited in the herbarium of the College of Forestry at Guangxi University.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Author details

[1]Guangxi Colleges and Universities Key Laboratory for Cultivation and Utilization of Subtropical Forest Plantation, Guangxi Key Laboratory of Forest Ecology and Conservation, College of Forestry, Guangxi University, Nanning 530004, China. [2]Guangxi Forestry Research Institute, Nanning 530002, China.

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