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INSIGHTS INTO BAMBOO SHOOT DEGENERATION

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Abstract

Bamboo shoot degeneration is a widespread phenomenon that can lead to bamboo forest loss and impaired sustainable management. However, little is known about the mechanisms of bamboo shoot degeneration. In this study, changes of morphology, anatomy and endogenous hormones were determined and analyzed at different degenerating stages of *Phyllostachys edulis* 'Pachyloen' shoot. The degeneration process was classified into different stages based on morphological changes of bamboo shoots. The stages were used as a basis for light microscopy study on the structure of the cells and enzyme-linked immunosorbent assay on the endogenous hormones. The observations indicated that the absence of guttation was the earliest and most remarkable feature of degenerating shoots with the cessation of height growth, followed by gradually withered sheaths and yellowed shoot bodies. A comprehensive judgement criterion was provided including morphological features and nutritional components. Anatomical analysis showed both cellular protection changes, such as cell wall relaxation and increased silica cells which might be the caused by water deficit, and senescence changes, like condensed and degraded nuclei in degenerating shoots. Furthermore, not only the contents of endogenous hormones but also ratios of growth-promoting hormones to ABA in both the whole bodies and different growing regions were remarkably different between the degenerating and normal shoot, which indicates that ABA accumulation might be induce and promote the degeneration of bamboo shoot. In addition, starch grains degradation increased, which might accelerate the degeneration of bamboo shoots. These findings reveal that bamboo shoot degeneration is a complicated process including senescence activities and stress response, which provides new insights into the mechanisms of bamboo shoot degeneration.

Key words: Bamboo shoot degeneration, Guttation, Bamboo sheath, Anatomical structure, Endogenous hormones, *Phyllostachys edulis* 'Pachyloen'.

Introduction

Bamboo is one of the most important forest resources with fast growth and high yield which are affected by the growth of bamboo shoot, especially the height growth. But some of bamboo shoots die naturally before growing into the adult, which is called bamboo shoot degeneration (Bai *et al*., 2011). The degeneration of shoot is a natural and universal phenomenon in bamboo. And the percentage of degenerating shoots of some species can reach as high as 80% dramatically reducing the outputs of bamboo shoot and culm severely threatening the sustainability of bamboo forest (Zhang & Tang, 2010; Bai *et al*., 2011; Chen *et al*., 2019).

Previous studies have reported that the nutritional values of degenerating bamboo shoots are still high, despite decrease in nutrient contents (Bai *et al*., 2011; Chen *et al*., 2019). Therefore, the earlier the degenerating shoot is identified, the higher its nutritional values are. However, it is difficult but necessary to distinguish the degenerating shoots from the healthy at the early stage of degeneration. Lu and Wu (1979) defined three stages of shoot degeneration of *Phyllostachys pubescens* mainly depending on the morphological characteristics. Guttation had been stopped naturally for 2-3 days, indicating the beginning of shoot degeneration and followed by the cessation of height growth. At this stage, the body of shoot was white and no insect damage. At the middle stage, the glossiness of shoot sheath decreased with slightly withered auricle and oral setae, and the shoot body became slightly yellow. Finally, the degenerating shoot had apparent morphological features: the shoot wrinkled and shrank with yellowed body, and even began to rot. Therefore, the absence of guttation has been regarded as a signature of the beginning of bamboo shoot degeneration. More evidences are needed to prove it.

Ding (2006) has suggested that bamboo shoot degeneration is a process of natural senescence based on the results that degenerating bamboo shoots had similar physiological characteristics to other premature senility plants, with enzymes activities decline (Chen & He, 1986) and DNase activity increase, resulting in a significant reduction of protein content and nucleic acids (Lu & Lin, 1982), then causing shoot growth to cease (Lu & Wu, 1979; Shen & Zhang, 1996). And the changes of endogenous hormones also showed the senescence signature that the content of growth-inhibiting hormones increased, while that of growth-promoting hormones decreased during bamboo shoot degeneration. All previous studies reported about bamboo shoot degeneration used the whole shoot as the materials. However, cells in different internodes of the same bamboo shoot, and even in different parts of the same internode, are at different developmental stages with specific structural, physiological and molecular features (Ding, 1997; Zheng *et al*., 1998; Xu, 2017).

In the present study, the morphological and anatomical structure features of bamboo shoots at different degeneration stages were investigated in *Phyllostachys edulis* 'Pachyloen', a variety of *Phyllostachys edulis* (Carr.) H. De Lehaie, has excellent shoot and culm with a thick wall. It shoots from March to April. The endogenous hormones were also analyzed in different parts of each internode of bamboo shoots during the degeneration. These studies will provide more evidences for identifying degenerating bamboo shoots and new insights into the mechanisms of the degeneration of bamboo shoots.

Materials and Methods

Experimental site and materials: Field experiments were conducted during the spring in 2017 and 2018 at the bamboo garden of Jiangxi Agriculture University, Jiangxi province, China (115°49'11″-115°49'23″ E, 28°46'00″-28°46'30″ N; elevation, 49.5 m). The experimental site was located in the humid subtropical climate, where the mean annual precipitation and temperature were 1567.7-1654.7 mm and 17-17.7 °C, respectively. The soil at the experimental site was red with slightly acidic.

Three normal and degenerating bamboo shoots with the same morphology, size, and height (20-30 cm) were collected, respectively. The top, middle, and base of bamboo shoot were cut to analyze the morphological and anatomical structure features, endogenous hormone contents at different degeneration stages. According Lu and Wu (1979), the shoot degeneration was classified into three stages: early stage, middle stage and late stage.

Morphological observations: We observed and photographed the sheath and shoot body of *Ph. edulis* 'Pachyloen' bamboo shoot, and measured shoot height in the morning every day, analyzing the morphological changes of bamboo shoots during the degeneration. Guttation was observed from 6:00 p.m. to the next 8:00 a.m. every day.

Anatomical characteristics: Fresh bamboo shoots with the same diameter and height at different development and degenerating stages were cut into about 1×1×1 cm sample and fixed in 70% FAA solutions (37% formaldehyde + acetic acid + 70% ethanol, volume ratio 1:1:18) at least two days. The samples were then dehydrated in an ethyl alcohol series (50, 70, 85, 95, 100, and 100%) for approximately 15-30 mins in each stage. After completely dehydrated, the samples were passed through xylene solutions (3:1, 1:1, 1:3, 100%, and 100%) for 20 minutes each time and then embedded in paraffin (Leica, 58-60℃). All sections of 8-10 μm thickness were cut using a rotary microtome (Leica RM2235, Germany), stuck onto carrier glass, and dried for two hours. Staining was performed with safranin O-fast green and mounted in neutral balsam. These sections were observed under a fluorescence microscope (Zeiss AX10, Germany), and photographs were taken with an attached camera system in the microscope.

Endogenous hormone determination: The extraction, purification, and determination of five endogenous hormones (IAA, ABA, GA_3, BR, ZR) in various tissues of *Ph. edulis* 'Pachyloen' during bamboo shoot degeneration stages by the enzyme-linked immunosorbent assay (ELISA) method were performed as described (He, 1993). 0.5 g bamboo shoots tissues of each sample were homogenized in liquid nitrogen and extracted at 4°C for four hours. The supernatant liquor was collected after centrifugation at 3500 r min^{-1} for 8 mins, and then the extracts were passed through a C-18 solid-phase extraction cartridge and dried in N_2. The supernatant solution was diluted with sample dilution for the endogenous hormones content determination.

Endogenous hormone contents of bamboo shoots at different developmental stages were measured according to the protocol described in Zhao *et al*., (2006). The logit curve was used to calculate the ELISA results, and the formula was described in Weiler *et al*., (1981):

$$\text{Logit } (B/B_0) = \ln\frac{B/B0}{(1-B)/B0} = \ln\frac{B}{B0-B}$$

B_0 is the chromogenic value of 0ng/ml, and B is the chromogenic value of other concentrations.

Statistical analysis: All of the data were the mean values from at least three independent experiments with three replicates in each experiment (means ± SD). The differences between means were statistically evaluated with analysis of variance (ANOVA) using SPSS 17.0 software. Duncan's multiple comparisons were used to test the difference significance, and differences were considered significant at $p<0.05$. Photoshop was used for image typesetting, and Origin 8.1 was used to draw charts.

Results

Morphology of *Ph. edulis* 'Pachyloen' shoots with degeneration: The normal shoots, with the increase in weight, had spread blades, orderly oral setae and elastic and bright white shoot bodies wrapped tightly by glossy sheaths. And there were liquid droplets exuding from the tips and edges of the blades from the late afternoon until the next morning (called guttation) (Fig. 1-a~a4). When guttation disappeared, the shoots stopped growing in height, and began to degenerate. The absence of guttation was the most conspicuous feature of the degenerating shoot at the early stage (Fig. 1-b~b2). Then the sheaths of the degenerating shoots lost their luster, the blades became hard and upright, and the oral setae became to wither and disorder. The shoot bodies yellowed and lost elasticity from the top with the degeneration (Fig. 1-c~c2). At late stage of degeneration, the shoots shrunk with loosed sheaths and rigid and yellow bodies, and some of them even began to rot (Fig. 1-d~d3).

Anatomical characterization of *Ph. edulis* 'Pachyloen' degenerated shoots: We further observed the cellular structure changes with the degeneration of bamboo shoots using the light microscope (Fig. 2). The results revealed the anatomical structures of the shoots had varied mainly in cell wall, nuclei and starch of different types of cells during the degeneration, although there was no significant difference between the shoot at the early stage and the normal. The cell walls in degenerating shoots had loosened gradually causing intercellular tight junction breakdown, and the borders between cells loss, and then leading to irregular shape and disorderly arrangement of the cells, even the degradation of the cell walls at late stage of the shoot degeneration. And also, more cell walls appeared silicified in the epidermis than those of the normal shoots, especially at late stage.

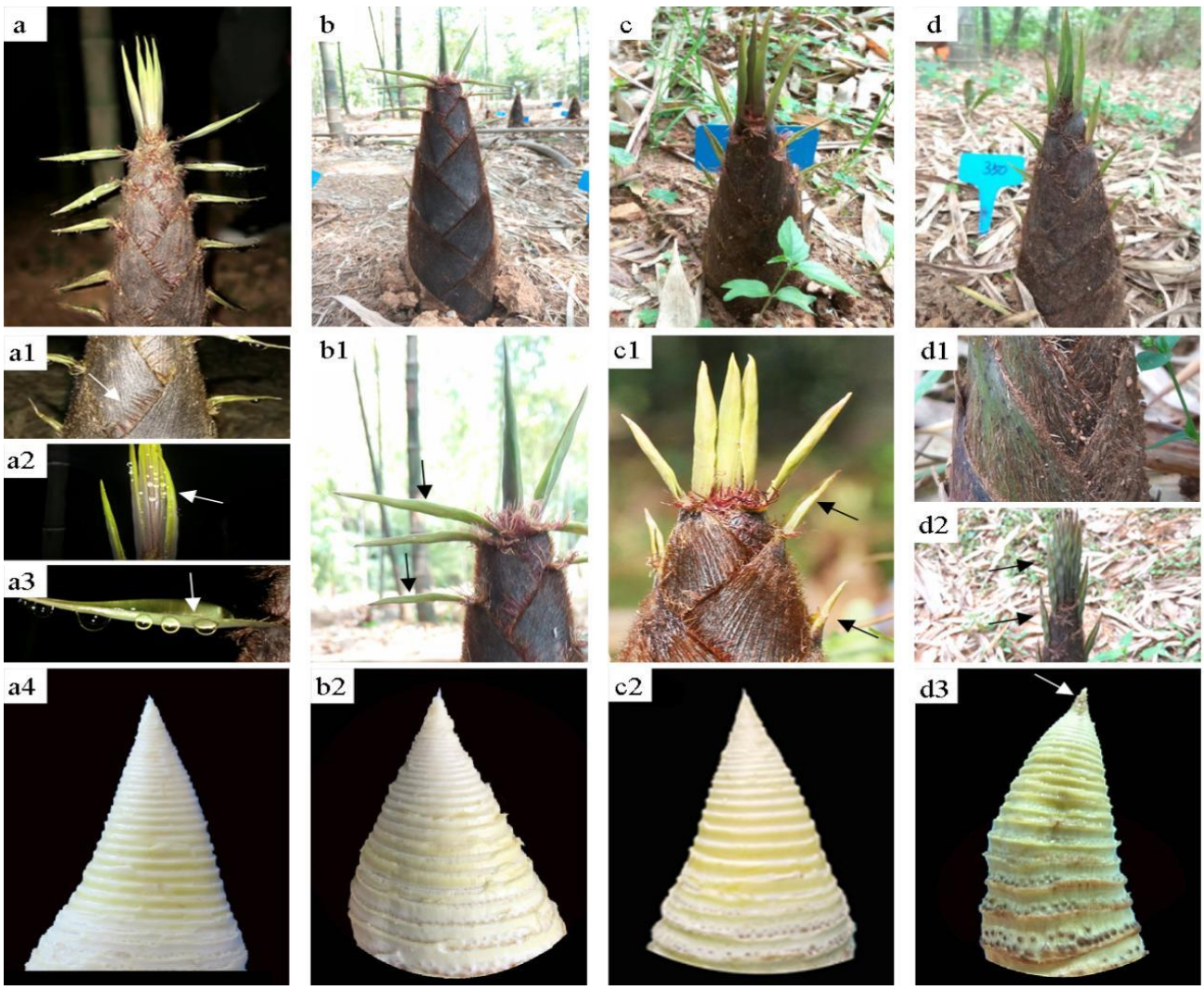

Fig. 1. Morphological changes of the normal and degenerating bamboo shoots. (a) Normal shoots. (a1-a4) The shoots had glossy sheaths that tightly wrapped around the body with spread blades, tidy oral setae, elastic and bright and white shoot bodies, and abundant guttation fluids on the edges of the blades in the early morning and at night. (b) Early degenerating shoots. (b1-b2) The absence of guttation was the most conspicuous characteristics. (c) Middle degenerating shoots. (c1-c2) The bamboo sheaths had lost their luster with hard and up-right blades and slightly withered oral setae. The shoot body became faint yellow, and its top was inelastic. (d) Late degenerating shoots. (d1-d2) The blades turned yellow, the oral setae were wilted and disordered, and the basal sheaths loosened. (d3) The shoot body was waxy yellow, rigid, and shrunk, and the top of the shoot appeared to have slightly rotted.

Figure 3 shows the changes of the nuclei in degenerating shoots at different stages, which had appeared irregularly shaped and marginally distributed with condensed or fragmented DNA, then degraded at late degeneration stage. Simultaneously, the cytoplasm in the shoots at late stage became transparent with light staining or no colour after stained with Safranine O-Fast green.

The intensity of starch fluorescence was detected using fluorescence microscope to reflect the content of starch in the cells (Fig. 4). The starch contents of bamboo shoots varied with both development and degeneration. In the normal shoots, the cells filled with the starch, and fluorescence intensity of the starch was the biggest at the meristematic stage, followed by a gradual decrease through the shoot development. However, there was a difference in degenerating shoots that starch contents increased at the beginning of cell elongation, although they showed the same general trends as observed in the normal shoots. Compared with the normal bamboo shoots, the starch contents in degenerating shoots decreased gradually from 58.07±15.79 of fluorescence intensity in normal shoots at the meristematic stage to 22.74 ± 2.98 at late degeneration stage (Table 1).

Table 1. Fluorescence intensity of starch grains of the normal shoot and degenerated shoot at different developmental stages.

The average number of starch grain	Normal shoots	Early degenerating shoots	Middle degenerating shoots	Late degenerating shoots
Meristematic stage	58.07 ± 15.79	42.62 ± 18.81	34.90 ± 4.33	22.74 ± 2.98
Initial elongation stage	50.80 ± 18.60	44.60 ± 11.49	37.60 ± 10.64	23.58 ± 4.53
Rapid elongation stage	43.12 ± 11.11	42.43 ± 10. 16	25.50 ± 11.10	12.64 ± 6.93
Late elongation stage	28.55 ± 7.20	19.13 ± 3.78	16.79 ± 4.30	13.51 ± 6.61

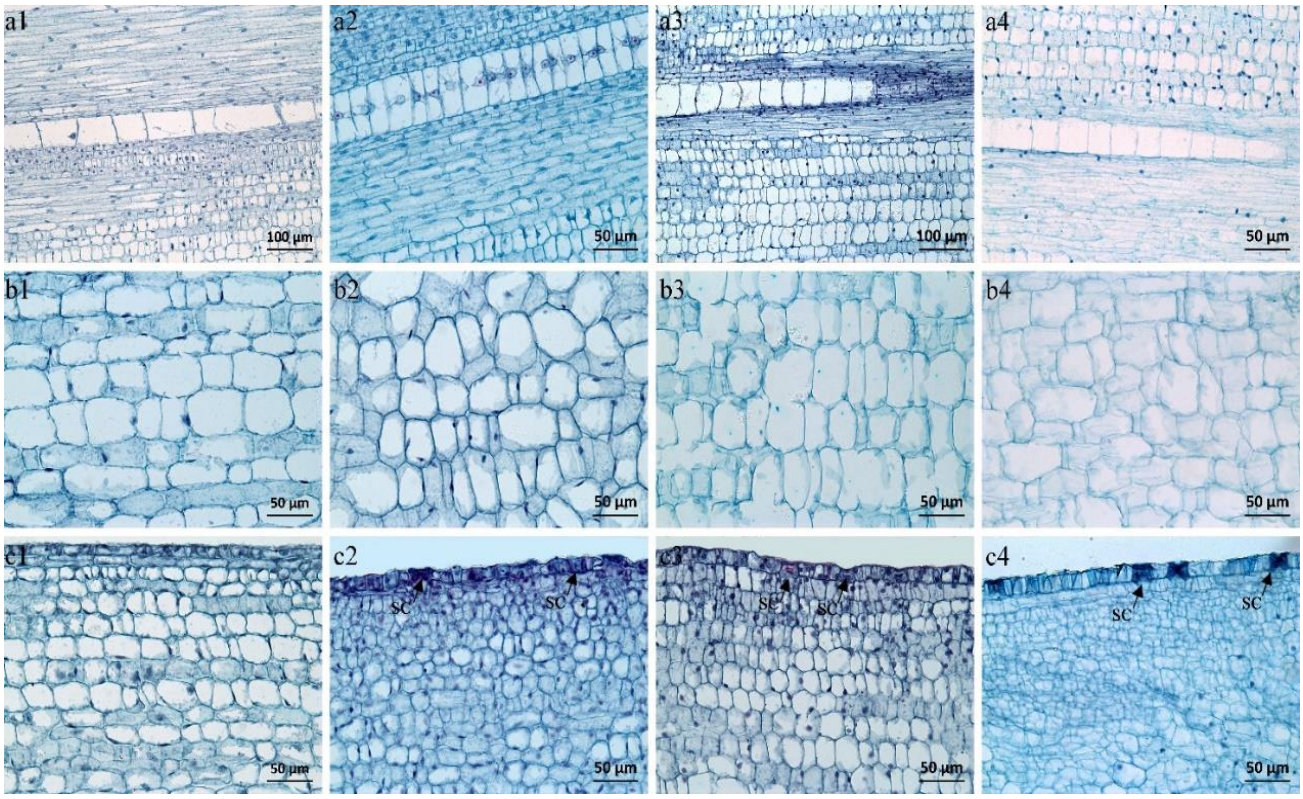

Fig. 2. Anatomical structure of cell wall of the normal and degenerating bamboo shoots (a. Fiber cell; b. Parenchyma cell; c. Epidermal cell. 1. Normal shoots; 2. Early degenerating shoots; 3. Middle degenerating shoots; 4. Late degenerating shoots). (a1-a4) The arrangement of fiber cells gradually loosened, and the cell transparency increased. (b1-b4) The arrangement of parenchyma cells gradually loosed, and the cell walls were seriously damaged during the late stage. (c1-c4) The number of silica cells (SC) in the epidermis increased, and the arrangement of the cells became disordered.

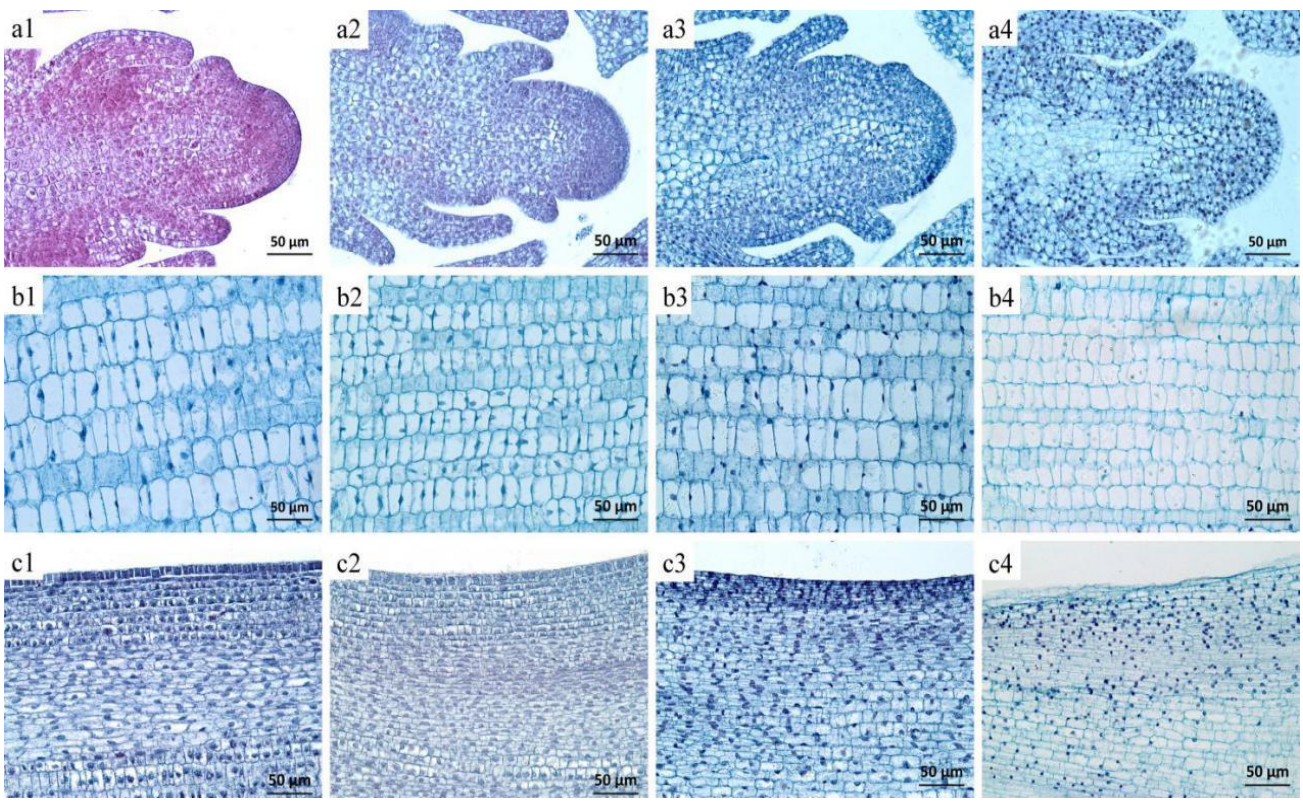

Fig. 3. Changes in the nuclei at different developmental and degeneration stages (a. Meristematic stage; b. Elongation stage; 1. Normal shoots; 2. Early degenerating shoots; 3. Middle degenerating shoots; 4. Late degenerating shoots) (a1-a4) The number of the nuclei in meristematic cells were gradually condensed and the nucleolar boundaries were gradually blurred. (b1-b4) Ground tissue cells elongated, and the nuclei were condensed, degraded, or unstained. (c1-c4) The cortical nuclei gradually condensed and edged, and the transparency of cells increased.

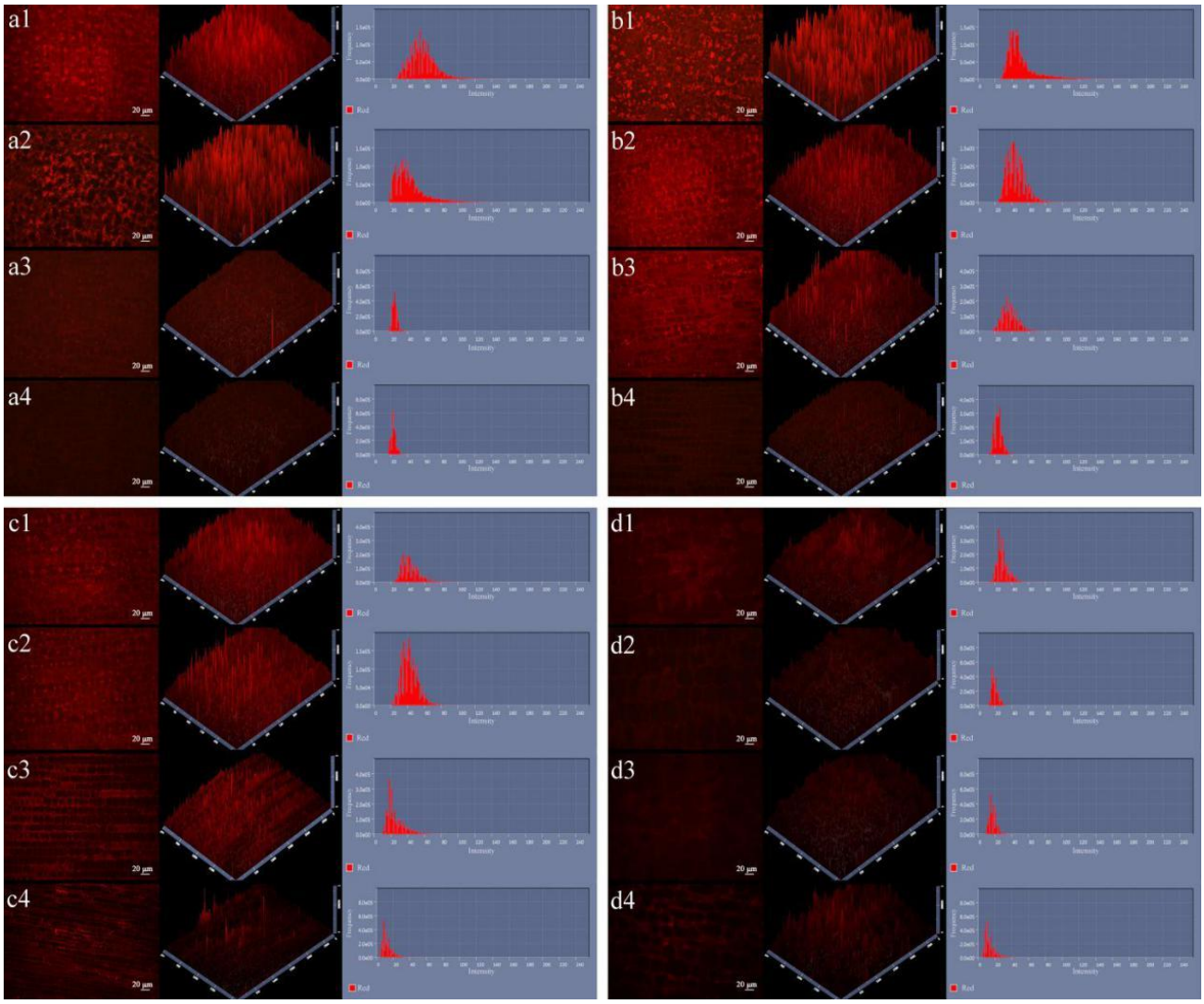

Fig. 4. The intensity of starch fluorescence in normal shoots and degenerating shoots at different developmental stages, and the contents decreased gradually with the degeneration: (a1-a4) Meristematic stage; (b1-b4) Initial elongation stage; (c1-c4) Rapid elongation stage; (d1-d4) Late elongation stage.

Changes of endogenous hormones during *Ph. edulis* 'Pachyloen' shoot degradation: The contents of endogenous IAA, ABA, ZR, BR, and GA_3 examined in degenerating shoots were all different significantly from the normal shoots, not only as a whole but also in different regions. Generally, endogenous ZR and GA_3 contents showed a decrease with the process of degeneration, while those of IAA, ABA and BR in degenerating shoots were higher than those of the normal, although the changes trends were a little different between them. Especially, endogenous ABA content had a very significant increase to 154.43 $ng \cdot g^{-1}$ FW at late stage of degeneration from18.95 $ng \cdot g^{-1}$ FW in the normal shoots (Fig. 5). And the ratios of growth-promoting to growth-inhibiting hormones, including IAA/ABA, GA_3/ABA, BR/ABA, ZR/ABA, (BR+GA_3+ZR)/ABA, and (IAA+ZR+BR+GA_3)/ABA, in degenerating shoots at various stages were lower than those of normal shoots, and decreased during the degeneration (Fig. 6). For different growing regions of the shoots, almost all endogenous hormones detected indicated the differences from the normal shoot during the degenerating, with the most significant content and change trend in the top and decreased differences from the top to the base of each degenerating shoot (Fig. 7).

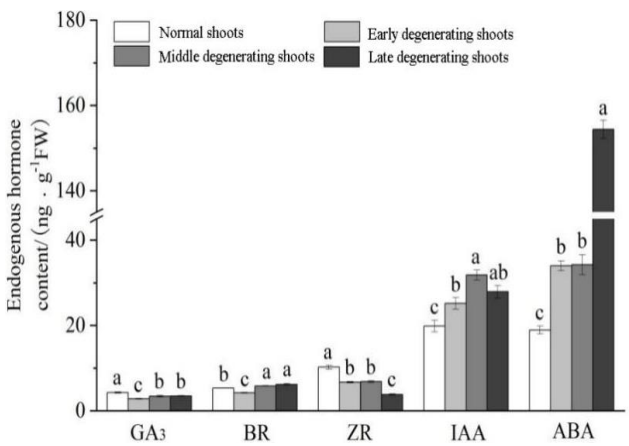

Fig. 5. Comparison of endogenous hormone contents between degenerating shoots and normal shoots of *Ph. Edulis* 'Pachyloen'. Note: the value represents the means ± SE; different lowercase letters indicate significant differences ($p<0.05$). The same for the below graphs.

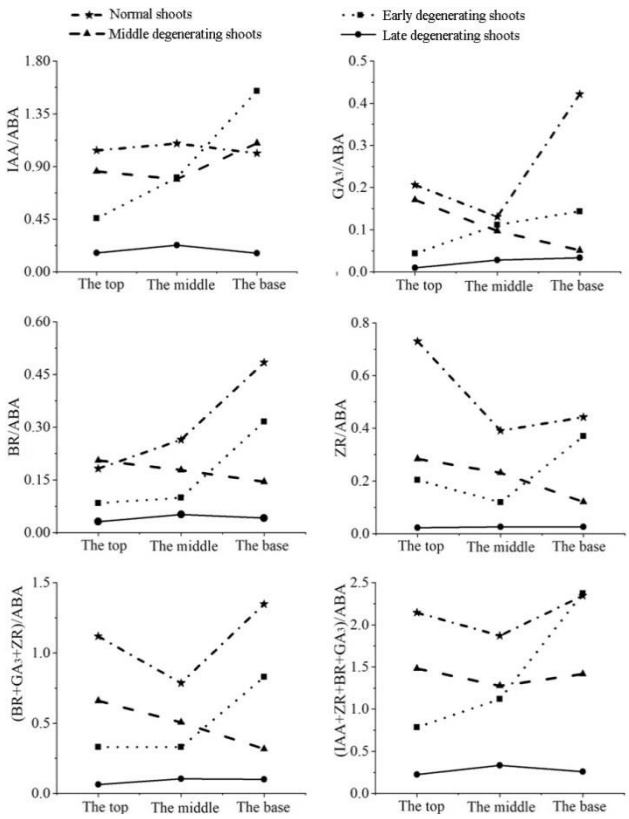

Fig. 6. Changes of endogenous hormone contents ratios in different parts of *Ph. edulis* 'Pachyloen' shoots during degeneration.

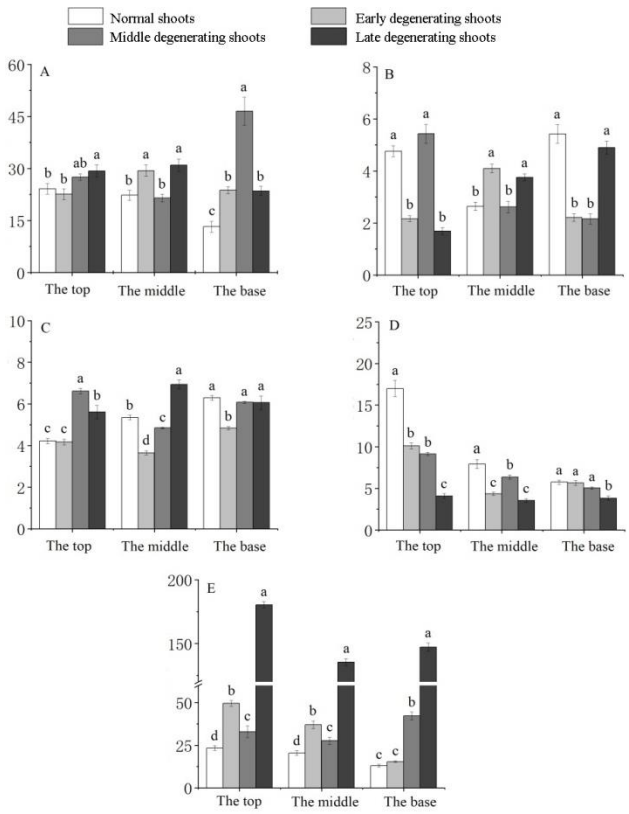

Fig. 7. comparison of endogenous hormone contents in different parts of degenerating shoots and normal shoots of *Ph. edulis* 'Pachyloen'.

Table 2. Changes of morphological characteristics and nutrient composition of *Ph. edulis* 'Pachyloen' during degeneration.

Different stages of degenerating shoot	Morphological characteristics					Nutritional components
	Guttation fluid	Bamboo sheath	Blade	Oral setae	Shoot body	
Normal shoots	Abundant	Glossy	Spread out	Regular	Stretchy; White and tender	High nutritional value, high contents of protein, amino acid, sugar and mineral elements
Early degenerated shoots	No guttation	Glossy	Spread out	Regular	White and tender; No difference from normal bamboo shoots	The nutrient contents are not much different from those of normal bamboo shoots
Middle degenerated shoots	No guttation	Wilted	Hard, small and erect	Messy	Inflexible; Dark yellow	Decreased contents of main nutrients
Late degenerated shoots	No guttation	Wilted	Unopened, withered and yellow	Dry and messy	Wizened; Wax yellow; Corruption at the tip	The main nutrient content has decreased, but it is still edible

Discussion

The identification of degenerating bamboo shoot is the premise of revealing the causes and underlying mechanisms, and it is critical for making full use of it. Guttation refers to the process of exudation of liquid droplets, loss of water from the tips, edges and adaxial and abaxial surfaces of uninjured leaves of plants (Singh, 2013; 2014a; 2014b), which is a common phenomenon in higher plants (Komarnytsky *et al*., 2000). Previous studies have showed that the plants with more water droplets exudated on the leaves have vigorous metabolism and grow faster, which indicates that guttation reflects the growth and development condition of the plants (Singh *et al*., 2016), and the bamboo shows the same tendency (Chen *et al*., 2019). Therefore, stopping guttation is the earliest visible feature for distinguishing the degenerating bamboo shoots. Our results proved remarkable changes in endogenous hormones contents after the stopping of exudation of water, although no obvious variation in anatomical structures at the early degenerating stage. The balance of water is important for growth and development of plants, resulting from the turgor pressure caused by water stress (Shao *et al*., 2008; Mcintyre, 2011; Tardieu *et al*., 2014; Sukiasyan, 2016). The unbalance of water metabolism in bamboo shoots might be the early response of the degeneration, which results in the water deficit of shoot bodies, leading to some changes in structure same as the influences of the drought, such as abnormal cell wall structure and increased silica cells in epidermis relating to prevent the loss of water. And the tissues of degenerating bamboo shoots took longer time to be dehydrated than those of the normal shoots, proving that the cell wall and silica cell variations because of the degeneration are benefit to water preservation.

Although the changes in morphological and anatomical structure were obvious, the degenerating bamboo shoots still were nutritious and edible, especially at the early stage. Our previous work on the nutritional components of *Ph. edulis* 'Pachyloen' shoots during the degeneration showed little differences in the contents of protein, amino acids, mineral elements, and other substances between early degeneration shoots and normal shoots (Chen *et al*., 2019). Other studies on other bamboo species revealed the same results (Bai *et al*., 2011). Therefore, the earlier the degenerating shoot is used for food, the higher nutritional value is. It is beneficial to form a comprehensive judgement combining nutritional components and morphological structure changes of the bamboo shoots with the degeneration for full use of the degenerating shoots. Table 2 shows morphological features and nutrient compositions of *Ph. edulis* 'Pachyloen' at different degenerating stages.

Bamboo shoot degeneration is considered a kind of self-regulation of bamboo forest, but the mechanisms remain unclear (Chen *et al*., 2001). Some researchers have suggested that bamboo shoot degeneration is premature senescence (Ding, 2006). This study showed that the nuclei were condensed, uncolored and transparent, and finally degenerated during the shoot degeneration, which is one of the most remarkable features of plant cell senescence, that is, nuclei DNA fragmentation and chromatin condensation (Gan, 2005; Liu, 2008).

Endogenous ABA is a signal and regulating factor inducing and promoting plant senescence (Zhang *et al*., 2012; Zhao *et al*., 2016). Our results showed that ABA contents increased significantly, even at the early stage, in both the whole bodies and different growing regions of degenerating shoots, and along with the decreased ratios of growth-promoting hormones to ABA, cell proliferation and elongation were inhibited (Lu, 2018). It appears that ABA accumulation in bamboo shoots might be an important factor that induces and promotes the degeneration of bamboo shoot. In addition, increased ABA can inhibit water absorption and create water deficits (Zhang *et al*., 2012), which lead to the shrinkage of the shoots and accelerate bamboo shoot degeneration.

Sugar is an important signal of plant cell senescence (Thomas, 2012), and its accumulation can trigger and accelerate plant senescence (van Doorn, 2008; Wingler *et al*., 2006). Starch grains, the main storage form of polysaccharides, provide materials and energy for plant growth and development. Therefore, the degradation of starch grains directly or indirectly participates in the regulation of plant senescence (Xiao *et al*., 2020). Our results showed that the content of starch grains in the degenerating shoots was lower than that observed in normal shoots and decreased gradually with degeneration. Increased degradation of starch grains might accelerate the degeneration of bamboo shoots. However, its mechanisms, such as whether the accumulation of sugar resulting from starch degeneration triggers the degeneration of bamboo shoots, remains unclear. Furthermore, whether genes that regulate starch degradation are involved in bamboo shoot degeneration remains unclear. These questions require further investigation.

Conclusion

In conclusion, the absence of guttation was the earliest and most remarkable feature of degenerating shoots with the cessation of height growth, followed by gradually withered sheaths and yellowed shoot bodies. A comprehensive judgment criteria of bamboo shoot degeneration was developed. Bamboo shoot degeneration is a complicated process including senescence activities and stress response, including cell wall relaxation and increased silica cells and condensed and degraded nuclei in degenerating shoots. ABA accumulation might induce and promote the degeneration of bamboo shoot. In addition, increased degradation of starch grains might also accelerate the degeneration of bamboo shoots. These findings provide new insights into the mechanisms of bamboo shoot degeneration.

Acknowledgements

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