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Article

Deciphering the Ramet System of a Bamboo Plant in Response to Intensive Management

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Abstract: Intensive management is a common practice in bamboo plantations to ensure higher shoot yields. However, the effects of these management practices on ramet systems are understudied. A pot experiment was conducted to explore the process of propagation for potted bamboo seedlings (*Phyllostachys praecox* C. D. Chu et C. S. Chao "Prevernalis") from a single mother bamboo to a ramet system exposed to a chronosequence of intensively managed bamboo forest soils. The ramet system of potted bamboo seedlings reached seven branching grades after two growth cycles. During ramet system expansion, the rhizome length and rhizome internodes decreased with increasing branching grade and the extension of intensive management periods. In the bud bank for each branching grade, the front branching grade was dominated by the bud output, which was conducive to consolidating the occupied living space. The back branching grade was dominated by bud input to continue rhizome penetration. With increasing branching, the mulching soil significantly inhibited rhizome bud germination and dormant bud accumulation. The mulching soil was not conducive to branch expansion in the ramet system, and ramet system expansion was predominantly based on the branching of the rhizome modules. With increasing branching and the extension of intensive management periods, rhizome branches decreased markedly. Our findings indicate that bamboo mulching inhibits branching and causes a differential reaction in branching types. The long-term mulching of bamboo forest soil was not conducive to the healthy and sustainable growth of bamboo. These results provide a basis for further research on the relationship between the bamboo ramet system and its productivity, as well as the population construction and maintenance mechanisms of bamboo ramet systems in the field.

Keywords: *Phyllostachys praecox*; rhizome; morphological growth; bud bank; branching

Citation: Gao, G.; Wen, X.; Wu, Z.; Zhong, H.; Zhang, X. Deciphering the Ramet System of a Bamboo Plant in Response to Intensive Management. *Forests* **2022**, *13*, 1968. https://doi.org/10.3390/f13111968

Received: 17 October 2022
Accepted: 19 November 2022
Published: 21 November 2022

1. Introduction

In clonal plants, the module hierarchy includes three levels, namely the genet (zygote development and formation), the clonal fragment (or ramet system), and the ramet (basic unit) [1,2]. In artificially managed bamboo forests formed by afforestation from seedlings, the closed bamboo population is formed through the continuous propagation of the seedling groups, known as genet groups. Therefore, the module hierarchy includes three levels, namely the genet, ramet system, and ramet. Artificially managed bamboo forests generated through bamboo mother plant afforestation predominantly include two levels of module hierarchy, namely the ramet and the ramet system. This is because it predominantly comprises ramet system groups formed by the expansion of different mother bamboos. Mother bamboo afforestation is relatively common in China. There are also differences among bamboo provenances [3–5], which leads to the uniqueness and complexity of the growth adaptation of bamboo populations in different environments. Therefore, implementing artificial optimization and the natural selection of bamboo populations at different levels, such as ramets, ramet systems, and genets, can become more complicated.

Bamboo forests are different from other tree species, and depending on whether it is a natural or an artificial bamboo forest, appropriate management is required to promote its sustainable use [6,7]. In the process of continuous renewal of the bamboo forests formed by either the genet group or the ramet system group, with natural death or manual cleaning of old bamboo stands and rhizomes, the original genet or ramet system will eventually disintegrate into several new bamboo ramet systems. After several years of growth, the bamboo forest becomes a collection of multiple clonal ramet systems formed by continuous aboveground and underground branching. These ramet systems are independent and interact with each other. Together, they build and maintain the development of bamboo forest populations, forming unique characteristics for bamboo population nutritional growth. However, many studies on growth and management technology in bamboo forests have focused on bamboo at the individual [8,9] and population [10–12] levels, and often exclude the study of the bamboo ramet system.

According to their different uses, bamboo forests include timber forests, bamboo shoot timber dual-use forests, and bamboo shoot forests [13]. Different bamboo forest types lead to different artificial management levels. Bamboo forests for shoots require high management intensity and have high yields and strong economic benefits. The mulching cultivation of bamboo forests requires high-intensity management [14]. This not only brings about considerable economic benefits but can also lead to adverse ecological consequences, such as bamboo forest decline and soil deterioration [15–17]. For bamboo forests under this high-intensity management, due to the frequent application of shoot picking, fertilization, reclamation, and the cleaning of old rhizomes [18], many underground rhizomes are broken. This results in the artificial fragmentation of the original ramet system. Therefore, research on the relationship between the ramet system and artificial management has a high scientific and application value [19–21].

Phyllostachys praecox C. D. Chu et C. S. Chao "Prevernalis" is an excellent small-diameter bamboo species for shoots. Mulching cultivation technology is widely used when it is being grown, and it is cultivated in the Jiangsu and Zhejiang Provinces of China and used as a "vegetable bamboo". There have been relatively few studies on the expansion of ramet systems and productivity control technologies in *Phyllostachys praecox* "Prevernalis" forests under high-intensity management. This study aims to explore the process of bamboo growth from the single mother bamboo to the ramet system using a controlled experiment with potted *Phyllostachys praecox* "Prevernalis" seedlings in a chronosequence of intensively managed bamboo soils. Given that the underground rhizome lateral buds are the source of aboveground bamboo ramets and underground bamboo rhizome branches [22], they play a crucial role in the formation of "bamboo ramet-ramet system-bamboo populations". Therefore, we analyze the relationship between different bamboo forest soils and the expansion of the bamboo ramet system by exploring underground rhizome morphological growth, bud bank dynamics, and lateral bud branching laws, during the expansion of the bamboo ramet system.

2. Materials and Methods

2.1. Test Location and Materials

The pot experiment with *Phyllostachys praecox* "Prevernalis" was carried out in the bamboo forest base of Lvjing village (30°43′ N and 120°30′ E), Jingshan Town, Yuhang District, Hangzhou City, Zhejiang Province, China. The test site is in the subtropical monsoon climate area, which is mild and humid with abundant rainfall. The average annual temperature is 16 °C, the average annual precipitation is 1837 mm, the average annual sunshine is 1970 h, and the frost-free period is 244 D. The soil is predominantly yellow and red soil with a fertile loose structure that is highly suitable for bamboo plant growth. Given the increasing impact of intensive bamboo forest management on bamboo forest soil and bamboo growth year by year [17], the soils used in the pot experiment were from a chronosequence of intensively managed *Phyllostachys praecox* "Prevernalis" plantations (0 (M0), 6 (M6), 12 (M12), and 18 (M18) years of cumulative mulching) with similar site conditions and management levels (Table 1). The intensively managed bamboo forests selected were initially mulched for three consecutive years and then rested for one year before being mulched for two consecutive years and then rested again for a further year. The soils were collected from above the 40 cm soil layer at a central position in the bamboo forest, with the residual bamboo rhizome and surface mulching residues in the soil being removed.

Table 1. Basic soil conditions of different potted bamboo seedlings.

Potted Soil	pH	Conductivity (μs·cm^{-1})	Organic Matter (g·kg^{-1})	Hydrolytic Nitrogen (mg·kg^{-1})	Available Phosphorus (mg·kg^{-1})	Available Potassium (mg·kg^{-1})
M 0	6.48	101.6	33.07	42.56	45.45	465.84
M 6	5.25	69.88	21.61	53.20	35.95	418.52
M 12	4.79	54.57	33.17	107.50	43.97	539.04
M 18	4.76	213.7	41.37	163.86	65.61	552.96

One-year-old healthy bamboo stands were randomly selected as potted mother bamboo in the un-mulched bamboo forest with a breast height diameter of approximately 3.50 cm (Figure 1). With the mother bamboo as the center, the soil around the mother bamboo was excavated at approximately 17 cm, digging downwards until no additional bamboo rhizome was found. The mother bamboo left 5–6 plates of branches, and the diameter of the soil was approximately 35 cm. The rhizome length from the mother bamboo needed to be more than 20 cm (the length of coming and going rhizomes was approximately 10 cm, respectively) to ensure that there were sufficient dormant buds on the bamboo rhizomes. After the mother bamboo had been excavated, it was important to remove the other residual and broken rhizomes in the soil to ensure that the newly germinated bamboo rhizomes and bamboo shoots were from the mother bamboo.

(a) (b)

Figure 1. Mother bamboo. (**a**) Artificial planting of mother bamboo for potting; (**b**) mother bamboo.

2.2. Experiment Design

The pot experiment was carried out in June 2019, and the root control container was an enclosed 100 cm (diameter) × 40 cm (deep) seedling pot. The soils from M0, M6, M12, and M18 were mixed well and used as the seedling substrate. Composted pig manure organic fertilizer was used in the pot experiment. The weight ratio of the substrate and the organic fertilizer was 8:1. The mother bamboo was planted in the center of the seedling pot with a planting depth of 25 cm, and each treatment had 25 reduplicates. After being planted in the pot, the bamboo seedlings were tied together using bamboo poles for wind support. The potted bamboo seedlings were uniformly exposed to natural light. During the seasonal water shortage period, water was poured evenly every 3–4 d. The growth recovery period for the potted bamboo seedlings was 5–6 months. From 2020 to 2021, the potted bamboo seedlings went through two complete growth cycles. In January 2022, the underground rhizome morphology, bud bank, and branch growth of the potted bamboo seedlings were investigated (Figure 2).

(**a**) (**b**)

Figure 2. Potting of mother bamboo and investigation of rhizome. (**a**) Potted mother bamboo; (**b**) sampling of rhizome.

2.3. Data Investigation and Analysis

2.3.1. Underground Rhizome Excavation

Six pots (six reduplicates) were randomly selected for investigation from the potted seedlings from each treatment. The pots were watered before opening the root control container to loosen the potted soil. The soil was then cleaned using a bamboo shoot spade and a small hoe. When the soil was loose, all the bamboo stands and the underground rhizomes were removed. The rhizomes were then washed with a high-pressure water pump and dried. The aboveground parts of the potted bamboo seedlings were then cut off, and the bamboo roots were trimmed with pruning shears.

2.3.2. Morphological Characteristics Investigation

The rhizome length (RL), rhizome diameter (RD), and rhizome internode number (RIN) were measured for each bamboo rhizome. The rhizome diameter was measured in the center of each bamboo rhizome using a vernier caliper. Statistical analyses were undertaken according to the branching grade (see branching growth investigation for details).

2.3.3. Bud Bank Investigation

The number of bamboo rhizomes and rhizome buds (total rhizome buds TRB), the number of bamboo stands and shoot buds (total shoot buds TSB), the number of dormant buds (DB), and the mortal buds (MB) germinated from the lateral buds of each bamboo rhizome. The sum of the numbers for all the bamboo rhizome lateral buds represented the total buds (TB). Among them, the TRB was the sum of the number of bamboo rhizome branches and the number of rhizome buds that showed pronounced differentiation and expansion. The growth direction of the rhizome buds was parallel to the horizontal plane, showing a trend of transverse growth in the soil. The TSB was the sum of the number of bamboo stands, and the number of bamboo shoot buds that showed pronounced differentiation and expansion. The growth direction of the bamboo shoot buds was perpendicular to the horizontal plane, showing a trend of vertical growth in the soil. The DB was small, white, or yellowish-white and full of vitality. The MB was blackened or decayed and hollow, completely losing its germination ability. The statistical analyses were undertaken according to the branching grade (see the section below for details).

2.3.4. Branching Growth Investigation

Each branch was marked as I branching grade, II branching grade, and III branching grade, according to the coming-to-going direction of the rhizomes. All the branches from the upper branching grade were considered as the next branching grade. The branch type for each branching grade was recorded, including the bamboo rhizome (Ra), rhizome bud (Rb), bamboo stand (Sa), shoot bud (Sb), and the total branching type (TT).

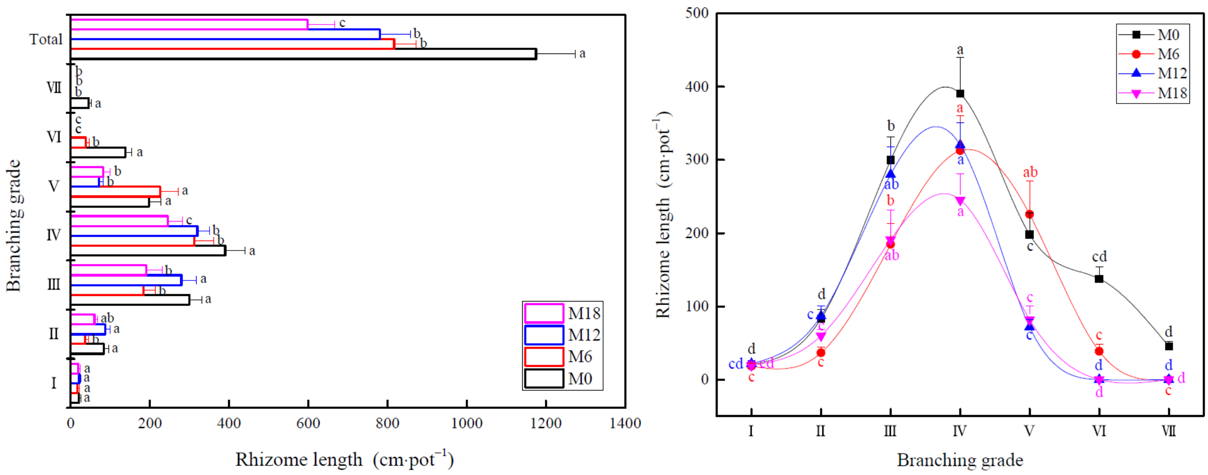
2.3.5. Data Analysis

The mean value and standard deviation of the data were calculated using Microsoft Excel 2016 (Microsoft Corporation, Redmond, WA, USA). One-way random block analysis of variance was performed using the SPSS 19.0 software (SPSS Corporation, Chicago, IL, USA). A Student–Neuman–Keuls test was used for multiple comparisons. Figures were produced using the Origin 2016 software (OriginLab Corporation, Northampton, MA, USA).

3. Results

3.1. Changes in Rhizome Morphology

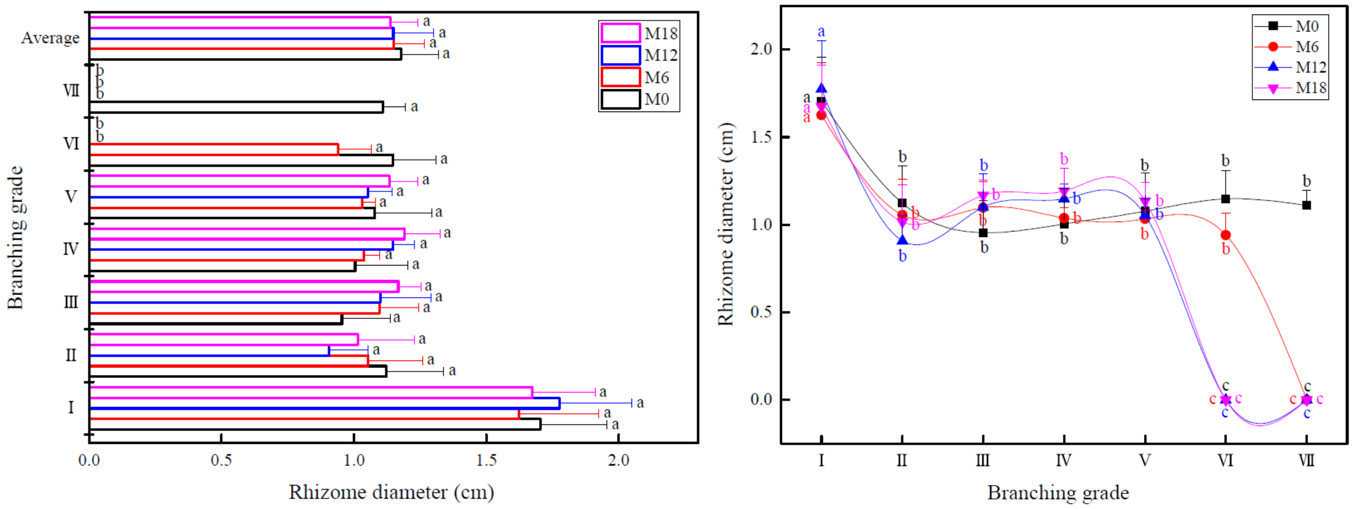
As shown in Figure 3a, no significant difference was observed in the rhizome length in the I branching grade among the four treatments. There were some significant differences in the II and III branching grades. From the IV to VII branching grades, the rhizome length significantly decreased with prolonged intensive management. The results also showed intensive management significantly decreased the total rhizome length in the following order: M0 > M6 ≈ M12 > M18. The bamboo rhizome length showed a parabolic distribution with increasing branching grade (Figure 3b), and there were distribution peaks for branching grade IV.



(**a**) (**b**)

Figure 3. Rhizome length. (**a**) Quantitative characteristics of rhizome length; (**b**) variation trend of rhizome length. Different letters indicate significant differences ($p < 0.05$).

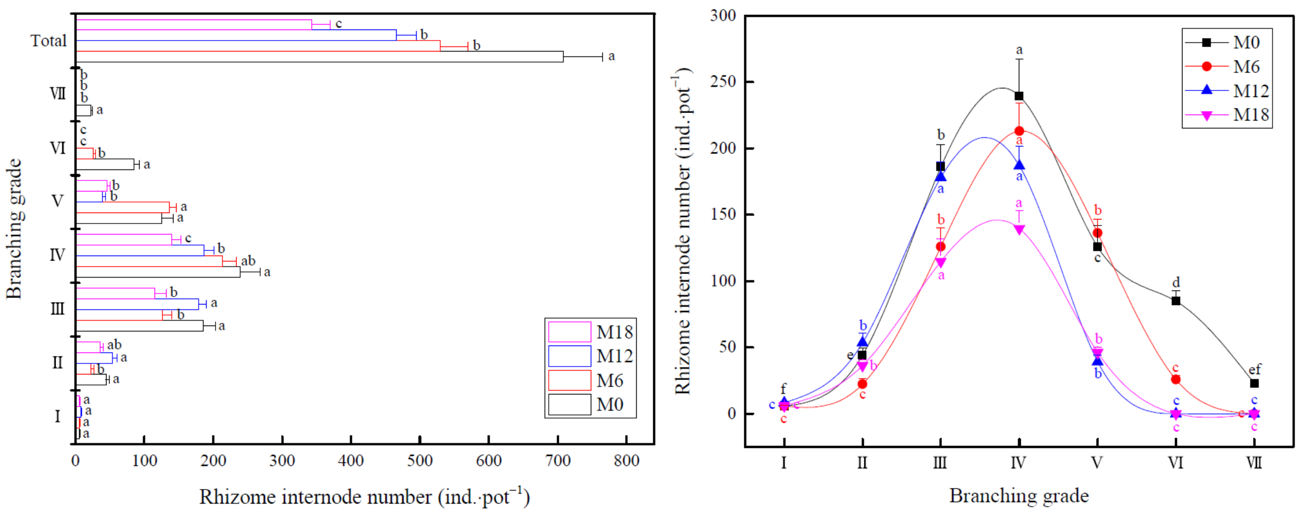
No rhizome growth was observed in the VI and VII branching grades following long-term mulching treatments, and there was no significant difference in the rhizome diameter among the other branching grades (Figure 4a). There was no significant difference in the average rhizome diameter for each treatment (Figure 4a). The rhizome diameter in each treatment from the I branching grade was more than 1.50 cm (Figure 4b), which was significantly higher than that of the II to VII branching grades. The rhizome diameters of the II to VII branching grades were distributed at approximately 1 cm, and there was no significant difference among the four treatments (Figure 4b).



(**a**) (**b**)

Figure 4. Rhizome diameter. (**a**) Quantitative characteristics of rhizome diameter; (**b**) variation trend of rhizome diameter. Different letters indicate significant differences ($p < 0.05$).

There was no significant difference in the number of rhizome internodes among the different treatments at the I branching grade (Figure 5a). Within the II and III branching grades, some significant differences were observed. From the IV to the VII branching grade, the number of rhizome internodes significantly decreased with the increase in intensive management periods. The number of rhizome internodes under different treatments showed a parabolic distribution with the increased branching grade (Figure 5b). The distribution peaks all appeared at branching grade IV.



(**a**) (**b**)

Figure 5. Rhizome internode number. (**a**) Quantitative characteristics of rhizome internode; (**b**) variation trend of rhizome internode number. Different letters indicate significant differences ($p < 0.05$).

3.2. Response of Rhizome Bud Bank of Bamboo Ramet System

Figure 6a shows that the number of different bud types in the potted seedlings at the I branching grade were not significantly different. At the II branching grade (Figure 6b), the values of TRB and DB in each treatment were generally higher than that of TSB and MB. At the III branching grade (Figure 6c), the DB values were significantly higher for all treatments than that of TRB, TSB, and MB. At the IV branching grade (Figure 6d), TRB, TSB, and MB were significantly lower than DB. The DB and TB of each treatment showed a decreasing trend with increasing intensive management periods. At the V branching grade (Figure 6e), TRB, TSB, and MB were significantly lower than DB. M0, M6 DB and TB were significantly higher than M12 and M18. At the VI branching grade (Figure 6f), M0 and M6 had bud banks and M12 and M18 had no bud banks. M0, DB, and TB were significantly higher than M6. At the VII branching grade (Figure 6g), only M0 had a bud bank, and there was only DB in the bud bank. In the total number of buds at different branching grades (Figure 6h), TRB, DB, and TB showed a decreasing trend with increasing intensive management periods.

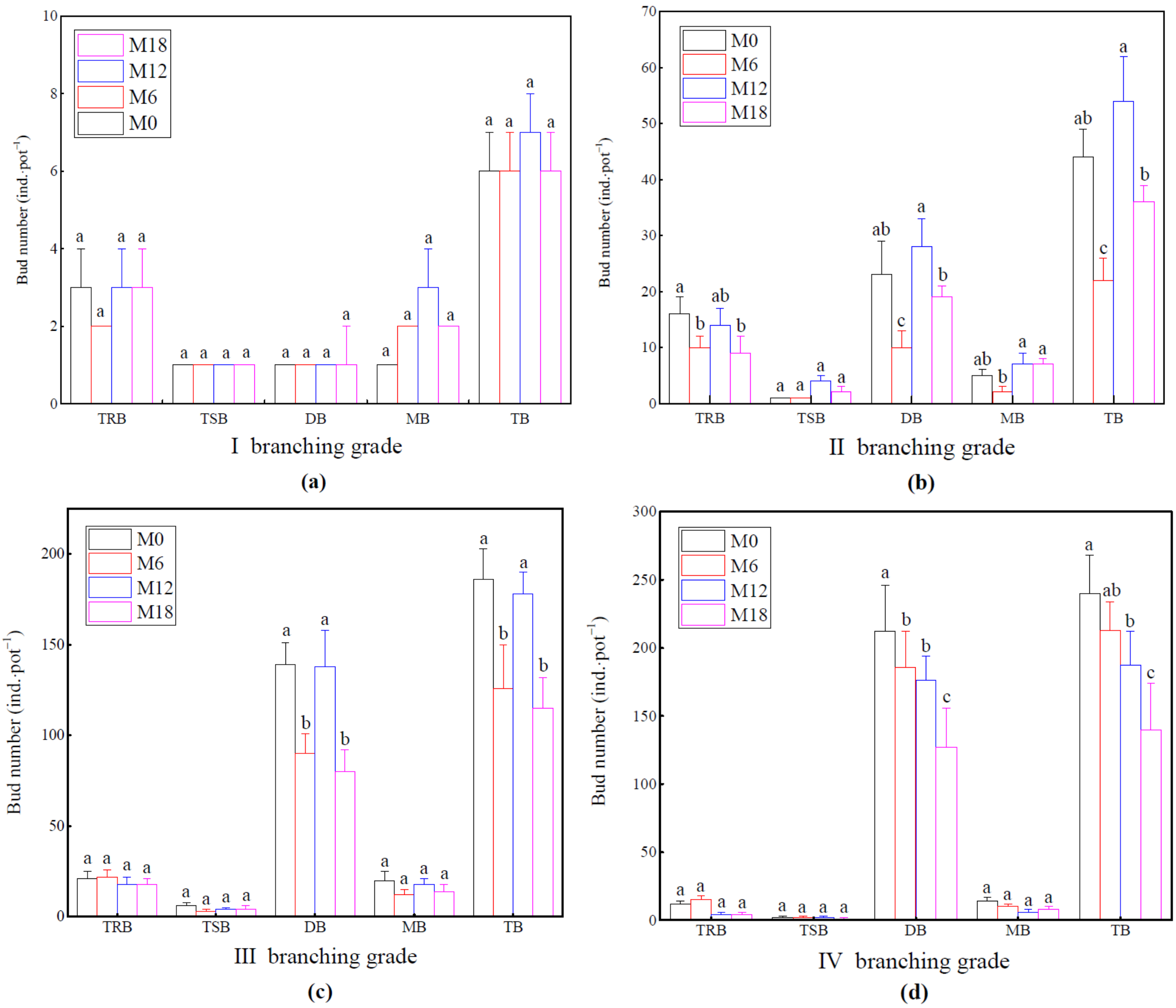


Figure 6. *Cont.*

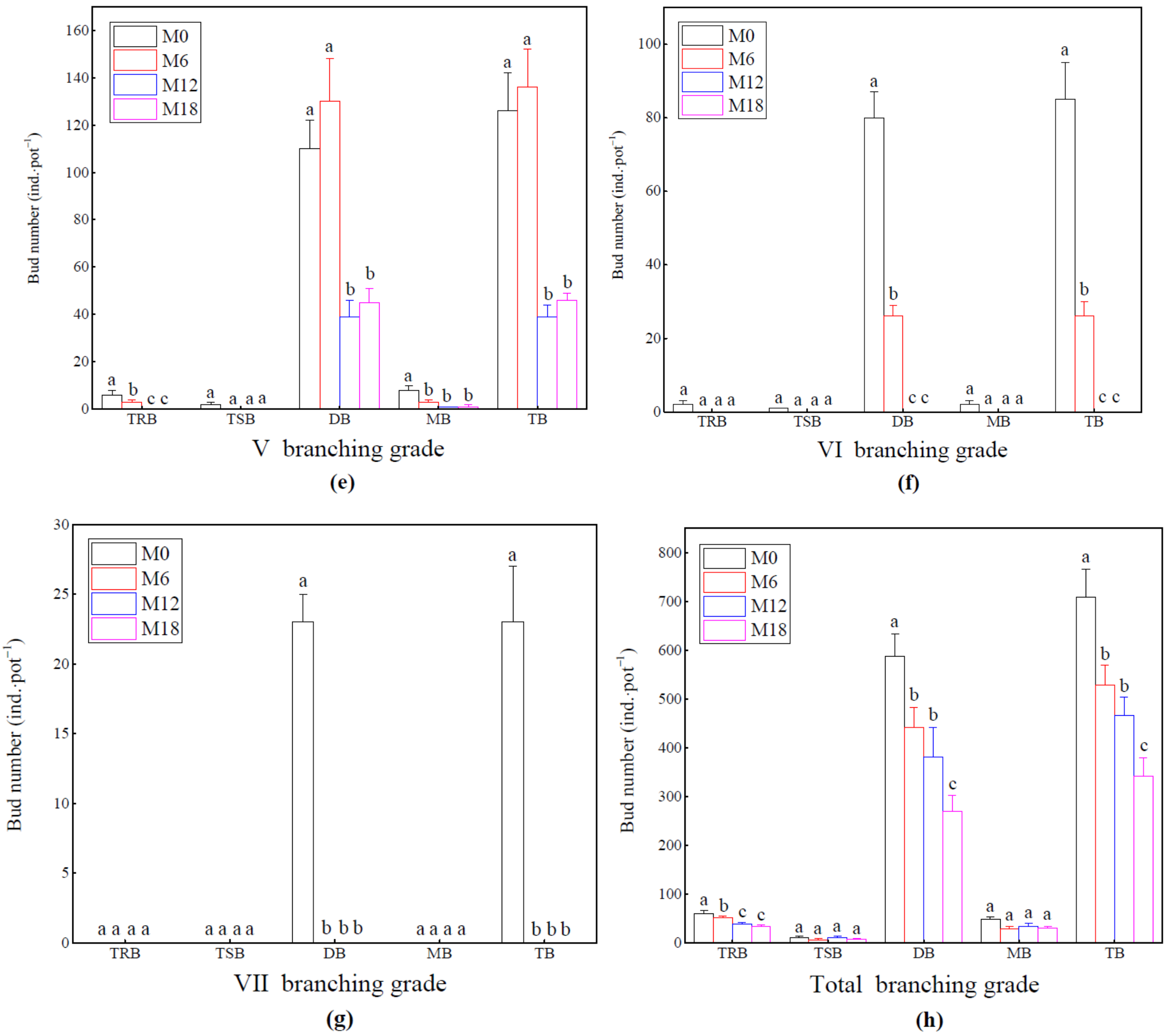


Figure 6. Quantitative characteristics of rhizome bud bank. (**a**) I branching grade; (**b**) II branching grade; (**c**) III branching grade; (**d**) IV branching grade; (**e**) V branching grade; (**f**) VI branching grade; (**g**) VII branching grade; (**h**) total branching grade. Different letters indicate significant differences ($p < 0.05$). TRB: total rhizome bud, it is the sum of rhizome and rhizome bud number; TSB: total shoot bud, it is the sum of bamboo stand and shoot bud number; DB: dormant bud; MB: mortal bud; TB: total bud.

According to Figure 7, with the increase in the branching grade, the TRB, TSB, DB, MB, and TB for each treatment showed a parabolic distribution. Among them, the parabola peaks for DB and TB in each treatment were above 100 individuals per pot and were predominantly distributed in the IV branching grade. The parabola peaks for TRB, TSB, and MB were all below 50 individuals per pot, and they were predominantly distributed in the III branching grade.

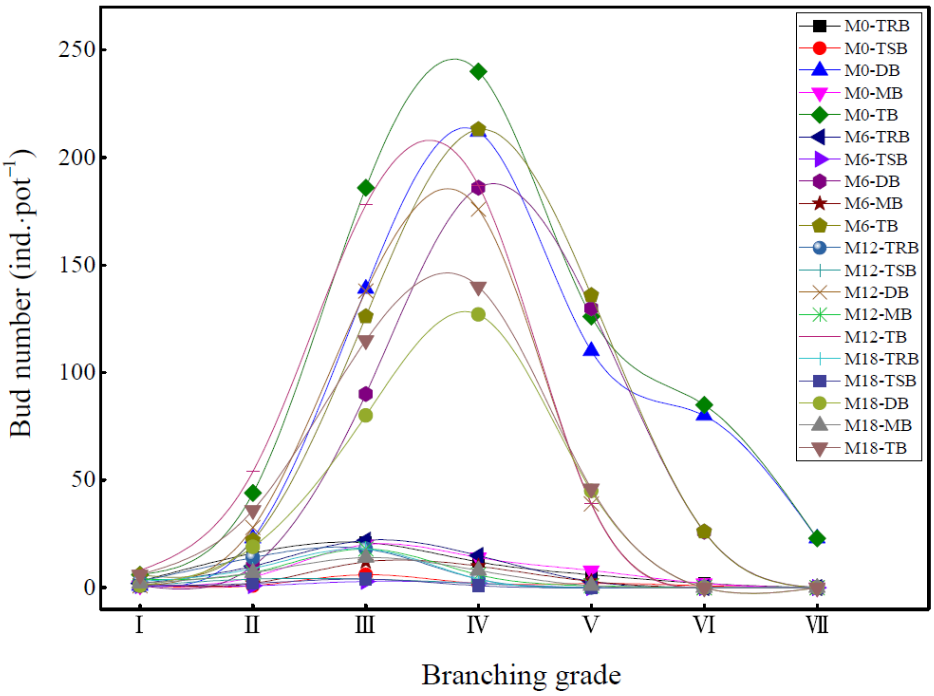
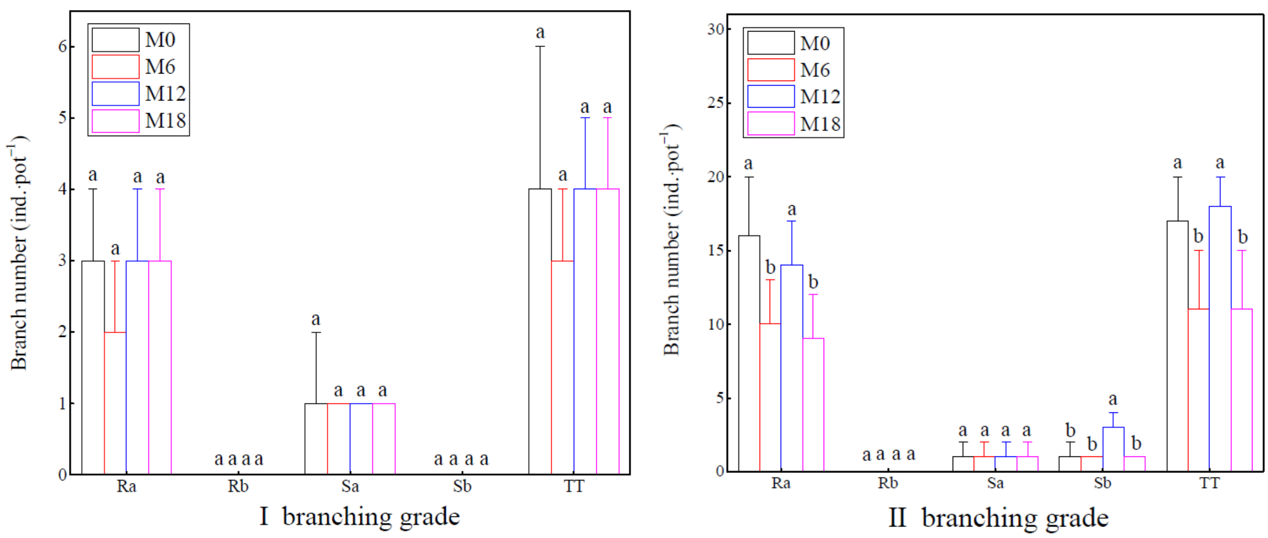


Figure 7. Variation trend of rhizome bud bank.

3.3. Branch Growth Difference of Bamboo Ramet System

As shown in Figure 8a, there was no significant difference in the number of different branch types in the I branching grade. At the II–III branching grades (Figure 8b,c), the Ra for each treatment was significantly higher than Rb, Sa, and Sb. The TT of the III branching grade showed a decreasing trend with increasing intensive management periods. At the IV branching grade (Figure 8d), M0, M6, Ra, and TT were significantly higher than M12 and M18. At the V branching grade (Figure 8e), M0, Ra, and TT were significantly higher than M6. At the VI branching grade (Figure 8f), only M0 had branches, and the number of branches was relatively small. The VII branching grade was found to be unbranched (Figure 8g). In the total number of branches at different branching grades (Figure 8h), Ra and TT were significantly higher than Rb, Sa, and Sb, and both showed a decreasing trend with the increase in intensive management periods.



(a) (b)

Figure 8. *Cont.*

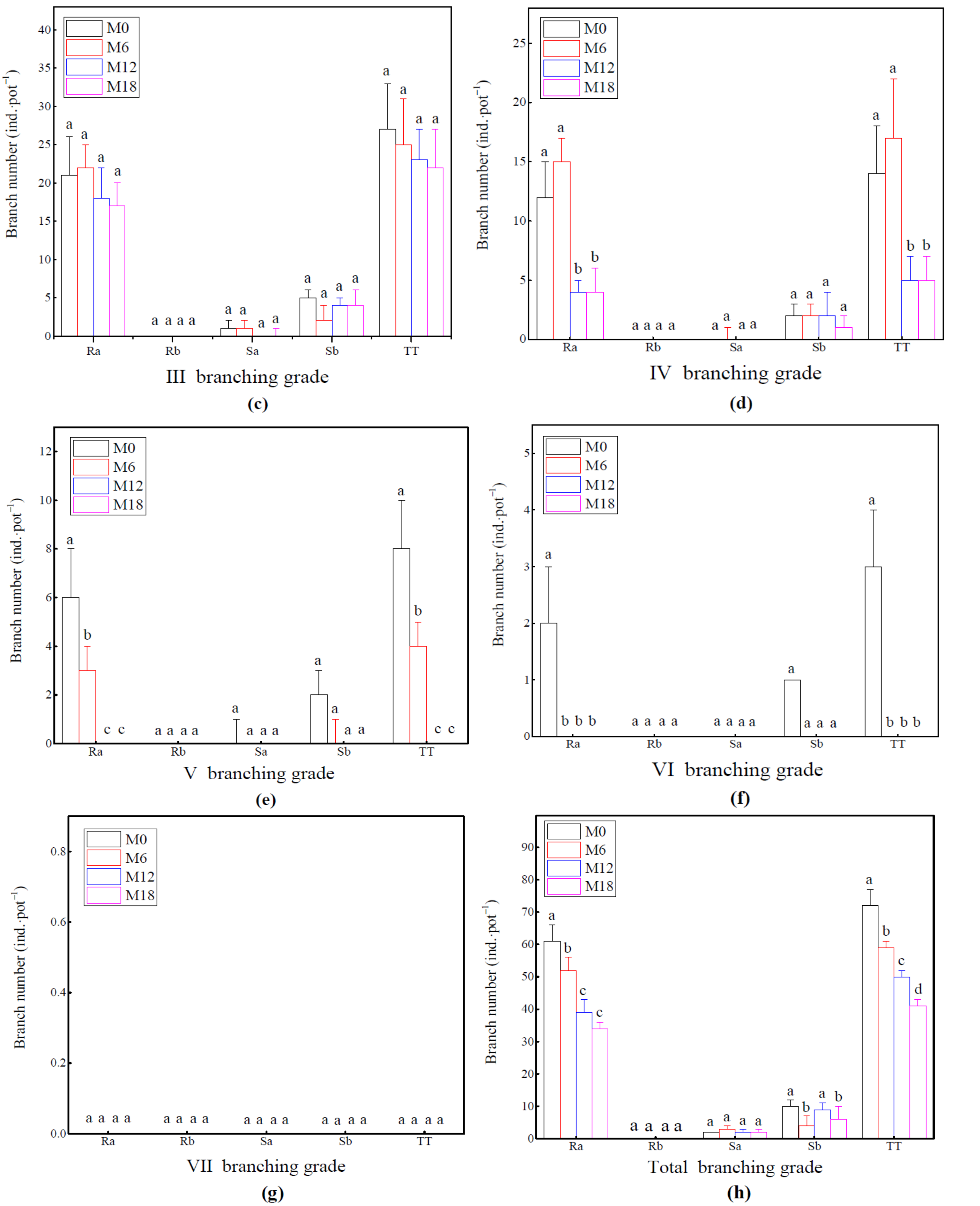


Figure 8. Quantitative characteristics of rhizome branching. (**a**) I branching grade; (**b**) II branching grade; (**c**) III branching grade; (**d**) IV branching grade; (**e**) V branching grade; (**f**) VI branching grade; (**g**) VII branching grade; (**h**) total branching grade. Different letters indicate significant differences ($p < 0.05$). Ra: rhizome; Rb: rhizome bud; Sa: bamboo stand; Sb: shoot bud; TT: total type.

With the increase in the branching grade (Figure 9), Ra, Rb, Sa, Sb, and TT showed a parabolic distribution for all the treatments. The peak values for Ra and TT in each treatment were above 15 individuals per pot. However, the peak values for Rb, Sa, and Sb were all below five individuals per pot. The peak value for each branch type was predominantly distributed in the III branching grade.

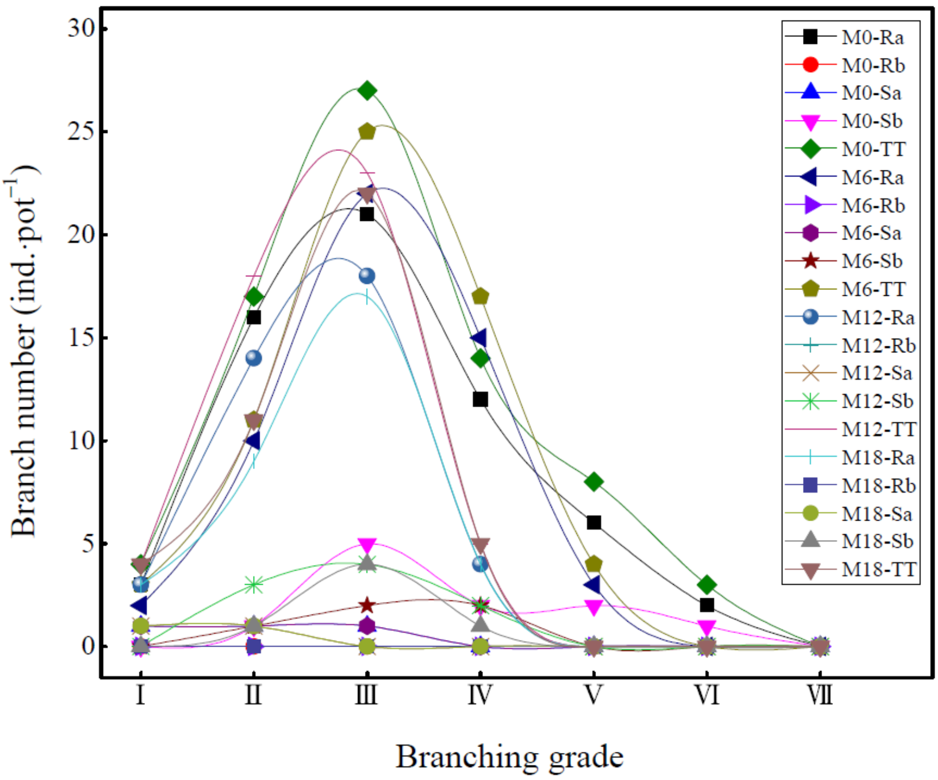


Figure 9. Variation trend of rhizome branching type.

4. Discussion

4.1. Effect of Intensive Management on Rhizome Morphology

With the continuous promotion of vegetative growth, the population number, and the distribution range of the clonal plants increased, and their growth space often continuously expands outward in a certain way and at a specific speed [23,24]. This influences the population distribution pattern for clonal plants at different times, in different spaces, and with different numbers. A single mother bamboo and a small segment of bamboo rhizome constituted the initial mother of the ramet system, which began to expand year on year after different growth seasons. With the increase in branching grade, the effect of the potted soil on the rhizome length and the number of rhizome internodes became increasingly pronounced. The longer the soil was mulched, the shorter the length of the bamboo rhizomes, and the lower the number of rhizome internodes. Due to severe soil acidification and other problems in perennial mulched bamboo forests [17], this should be an important reason for inhibiting the expansion of potted seedlings. In this study, we found that among all the branching grades, the middle branching grades formed the main component of bamboo rhizome growth. To adapt to different environments and promote population development, the greater the number of different modules of the clonal plant population, the greater the contribution rate to the population [25,26]. This shows that the middle branching grades are the main contributor to the expansion of bamboo rhizomes. After the bamboo seedlings were potted, the diameter of the new bamboo rhizomes became smaller, but they were not substantially affected by different soils. This may be caused by the growth restriction of potted plants, or it may be a general growth phenomenon at the beginning of the expansion of the mother bamboo ramet system.

4.2. Effect of Intensive Management on Rhizome Bud Bank

Underground bud banks play a crucial role in plant population expansion, community dynamics, and the functional response of ecosystems to environmental changes and disturbance [27]. Bamboo ramet systems can continuously expand their living space through branch growth of the bud bank. The general spatial expansion behavior of clonal plants is initially manifested in the continuous consolidation of occupied space and the potential expansion of unoccupied space by the formation of potential populations with high viability [28]. This study found that in the bud bank of each branching grade, the peak of germinated and mortal buds was predominantly distributed in the middle and front branching grades. The peak of dormant buds was mainly distributed in the middle and back branching grades. This shows that the front branching grades are dominated by the bud output, and the back branching grades are dominated by the bud input. In this way, the front branching grades of the bamboo ramet system continue to consolidate the occupied space, while the back branching grades continue to occupy new living spaces. The formation and development of underground buds for clonal plants are easily affected by environmental factors. Soil is an important factor affecting the establishment and dynamics of underground plant bud banks [29]. This study found that during the expansion of the ramet system, the lateral buds of the underground rhizomes were predominantly sprouting rhizome buds. With the increase in the branching grade, the number of dormant buds increased considerably and became the main body of the total number of buds. Mulched soil significantly inhibited the germination of rhizome buds and the accumulation of dormant buds. This resulted in the decrease of total buds with the increase in intensive management periods, which is consistent with the research conclusions of Gao [22]. At the back branching grades, the bud bank of potted seedlings in the mulched soil gradually disappeared, and finally, only potted seedlings in un-mulched soil had a bud bank, and there were only dormant buds in the bud bank. Changes in the soil nutrients and properties affect the physiology or morphology of plants [30,31]. Over the long term, mulching the soil is not conducive to branching and expansion in bamboo ramet systems.

4.3. Effect of Intensive Management on Branch Growth

To better survive and adapt to the environment and successfully complete the life cycle process, clonal plants can change their growth characteristics and make trade-offs and adjustments by adjusting the material and energy distribution among modules [2]. In this study, the expansion strategy of the bamboo ramet system in potted seedlings predominantly selected the branch of the bamboo rhizome module, and its branches were mainly distributed in the middle and front branching grades. This is consistent with the conclusion that the front branching grades are dominated by the bud output. The growth of clonal plants is a process in which different organs are constantly changing in the environment [32]. The adjustment and adaptability of clonal plant morphological construction include the interaction between the morphological structure of individuals and clonal fragments, namely the ramet system, at two levels and in the environment [33]. The branching method of the bamboo ramet system in potted seedlings was highly conducive to realizing its rapid expansion. With the increase in the branching grade and the extension of intensive management periods, the effect of soil on bamboo rhizome branching was relatively pronounced. The difference in other branch types was not significant, and the number of branches gradually decreased until there were no branches. This indicated that mulching soil not only inhibited branching but also led to the differential reaction in branching types. Most plant modules have a significant correlation and stable growth relationship, which reflects the cooperative growth strategy between modules [34]. The synergy of quantitative characteristics between the different modules has gradually formed a functional combination that can successfully adapt to the environment [35]. The coordinated development between modules realizes the regulation of plant survival, growth, and reproduction, and makes various functional processes reach the most effective state [2]. The reduction in bamboo rhizome branches and the differential reaction of the branch type in the mulched soil fully reflect the adaptive feedback of the synergistic changes in the branch modules of the bamboo ramet system in the soil.

5. Conclusions

During the development of the potted seedling ramet system in different soils, with an increase in the branching grade and the extension of intensive management periods, the length of the bamboo rhizomes was reduced, and the number of rhizome internodes decreased. Among all the branching grades, the middle branching grades contributed the most to the expansion of the bamboo rhizomes. The smaller rhizome diameter of the potted seedlings may be an adaptive way for the intensity of foraging of the bamboo ramet system. In the bud bank of each branching grade, the front branching grades were dominated by the bud output, which was conducive to consolidating the occupied living space. The back branching grades were dominated by the bud input, to continue to occupy new living space. With the increase in the branching grade, mulched soil substantially inhibited the germination of rhizome buds and the accumulation of the dormant buds. The mulched soil was not conducive to the branching and expansion of the bamboo ramet system. The development of the bamboo ramet system for potted seedlings was dominated by the branching of bamboo rhizome modules. With the increase in the branching grade and the extension of intensive management periods, mulching soil not only inhibited branching but also caused the differential reaction in branching types. The branching growth of the bamboo ramet system is easily affected by the underground rhizome morphological structure, bud bank dynamics, growth phenology, bamboo ecological adaptability strategies, and other factors. Therefore, it is necessary to conduct more in-depth research.

Author Contributions: Conceptualization, G.G. and X.Z.; investigation, G.G., H.Z., X.W. and Z.W.; writing—original draft preparation, G.G.; writing—review and editing, X.Z. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Fundamental Research Funds of CAF (CAFYBB 2021QB007), the National Natural Science Foundation of China (32001378), and the Talent Development Program of China National Bamboo Research Center (ZXPT202201).

Data Availability Statement: Data are available from the authors on request.

Acknowledgments: We thank all staff of zhangxingshan family farm in Yuhang, Zhejiang, China for their assistance.

Conflicts of Interest: The authors declare no conflict of interest.

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