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Breeding Strategies and Utilization of *Phyllostachys edulis* for Shoot and Timber Production

Wenzhong Huang, Zhongmei Hong
CRO Service Station, Sanya Tihitar SciTech Breeding Service Inc., Sanya, 572025, Hainan, China
Corresponding email: wenzhong.huang@hitar.org

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Abstract This study expounds the breeding methods and current situation of the utilization of *Phyllostachys edulis* for shoot and timber production. In recent years, technologies such as molecular breeding and gene editing have brought new ideas to the breeding of new *Phyllostachys edulis* varieties and the improvement of their traits. The research found that through transcriptome and small RNA sequencing, some key genes and miRNAs that affect the growth, lignification and primary thickening of bamboo shoots were identified, and their regulatory networks were also analyzed. Hormone signaling, carbon metabolism and cell wall synthesis all play important roles in the rapid growth and material property formation of *Phyllostachys edulis*. Research on some specific varieties, such as *Phyllostachys edulis* 'Pachyloen', has also revealed the molecular mechanisms underlying their high-yield and high-quality traits. This research aims to provide theoretical support for the breeding of high-quality *Phyllostachys edulis* for shoot and timber production and the sustainable development of the industry.

Keywords *Phyllostachys edulis*; Molecular breeding; Gene editing; Rapid growth; Lignification

1 Introduction

Phyllostachys edulis is one of the most important dual-purpose bamboo species in the world. It is mainly distributed in subtropical regions and has the largest planting area in China. *Phyllostachys edulis* not only provides two types of raw materials, namely bamboo shoots and bamboo materials, but also has significant value in terms of ecology, economy and culture. Approximately 2.5 billion people worldwide rely on bamboo resources, and the annual trade volume of the bamboo industry is close to 2.5 billion US dollars. As a dominant species, *Phyllostachys edulis* plays an irreplaceable role in regional economy and sustainable development (Hu et al., 2020; Gao, 2021; Chen et al., 2022).

Phyllostachys edulis can produce both bamboo shoots and high-quality timber, but it is not easy to ensure both high-yield bamboo shoots and high-quality timber during breeding. Increasing the yield of bamboo shoots often affects the quality of timber, such as wall thickness, fiber length and lignin content. The biological characteristics of *Phyllostachys edulis* also add to the difficulty. It rarely flowers, and the flowering is irregular. The generation cycle is also very long, which makes traditional hybrid breeding difficult to carry out (Hu et al., 2020; Gao, 2021). In addition, the lignification process of bamboo involves multiple signaling pathways and metabolic pathways, and the regulatory network is very complex, which makes it more difficult to simultaneously improve the yield and quality of bamboo shoots (Yang et al., 2021; Chen et al., 2022; Li et al., 2022).

This study compiles the research progress on the dual-purpose breeding of *Phyllostachys edulis* for shoot and timber production, introduces the multi-faceted value and utilization of *Phyllostachys edulis* in the industry, analyzes the main scientific and technological challenges faced in breeding, and also explores how new technologies such as molecular breeding and gene editing can help break through the limitations of traditional breeding and promote the coordinated improvement of bamboo shoot yield and material quality. This research aims to provide theoretical and technical support for the efficient utilization and sustainable development of *Phyllostachys edulis*.

2 Biological and Economic Basis of *P. edulis*

2.1 Growth characteristics and ecological adaptability

Phyllostachys edulis is famous for its fast growth and strong adaptability. Studies show that its maximum daily growth rate can reach 114.5 cm, which is much higher than that of most plants. The growth of *Phyllostachys edulis* can be divided into three stages: cell division, cell elongation and secondary wall thickening. This process is regulated by multiple hormones, such as gibberellin, cytokinin, abscisic acid and auxin, and is also easily affected by temperature and mechanical pressure (Figure 1) (Zhang et al., 2018; Lan et al., 2020; Chen et al., 2022).

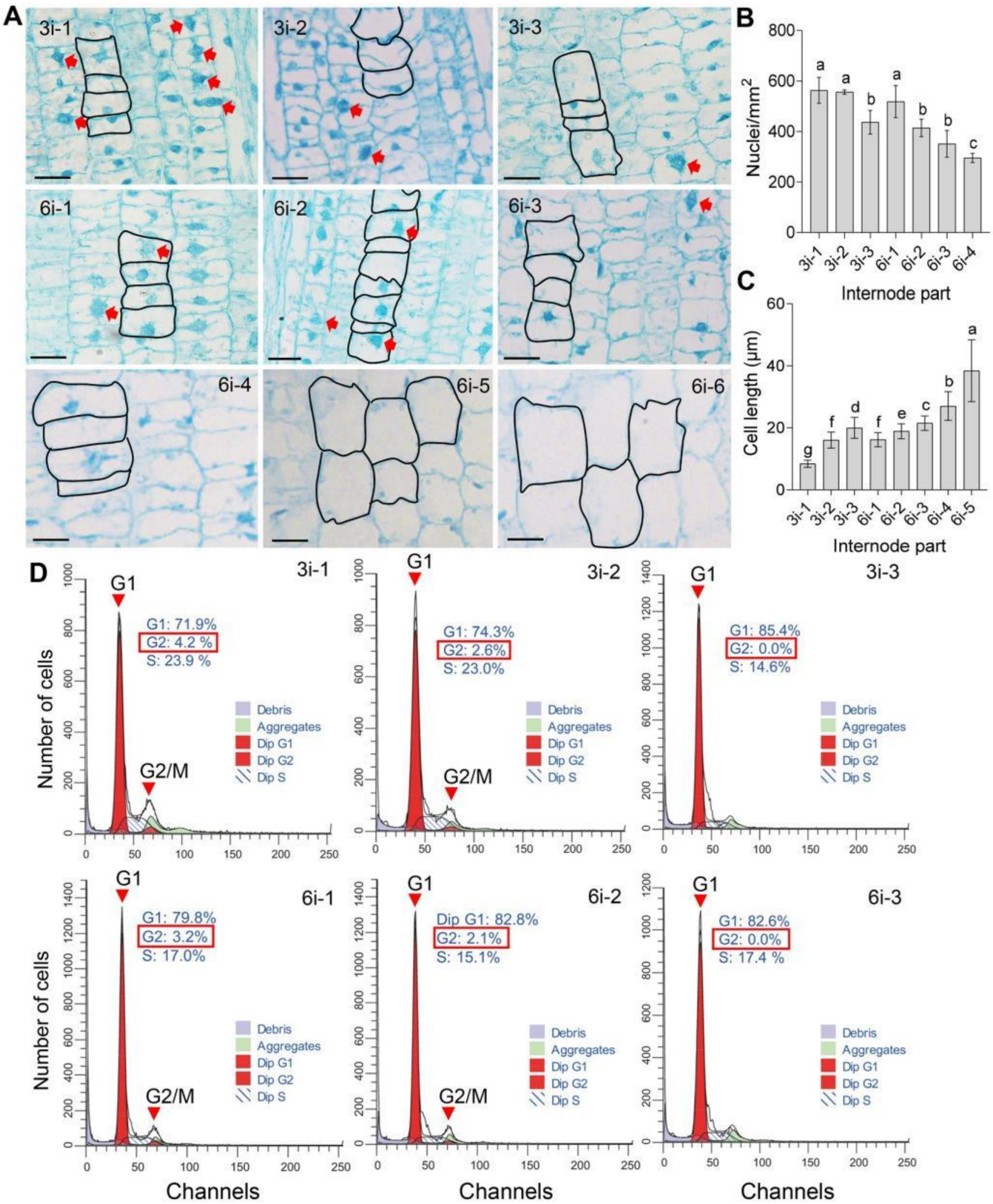

Figure 1 Sectionalized growth in internode 18 of *P. edulis* (Adopted from Chen et al., 2022)

Image caption: A-C, Parenchyma cell morphology (A), number of nuclei (B), and cell length (C) of the first (3i-1), second (3i-2), and third (3i-3) segments of the 3-cm-long 18th internode and the first (6i-1), second (6i-2), third (6i-3), fourth (6i-4), fifth (6i-5), and sixth (6i-6) segments of the 6-cm-long 18th internode. Parenchyma cells in (A) are indicated by enclosed lines, and arrows indicate mitotic figures. Scale bar = 50 μm. Data shown in (B) and (C) are means ± sd ($n \geq 180$ for cell length; $n \geq 6$ for nucleus density). The different letters (lowercase) in each column indicate significant differences at $P < 0.05$. D, Flow cytometry analyses showing nucleus status of parenchyma cells in each of the 1-cm-long sections of the 3- and 6-cm-long 18th internodes. G1, G2, S, and M in the flow cytometry channels represent Gap1, Gap2, synthesis, and mitosis stages of mitotic cell division (Adopted from Chen et al., 2022)

Phyllostachys edulis also has a well-developed underground rhizome system, which can efficiently store and transport nutrients. Studies have found that the carbon distribution of newly rooted rhizomes accounts for 9.5% of the total biomass, which is much higher than that of woody plants of the same size (Kobayashi et al., 2022). It has a strong adaptability to NH_4^+ in nitrogen fertilizers and performs better and has stronger competitiveness in a high ammonia environment (Zou et al., 2020; Hong et al., 2024). In addition, *Phyllostachys edulis* can improve soil water retention and increase microbial diversity by regulating rhizosphere microorganisms and soil properties, thereby enhancing the stability of the ecosystem (Liu et al., 2023; Fang et al., 2024).

2.2 Economic value of bamboo shoots as food

Bamboo shoots are important cash crops. They grow fast, have high yields and are rich in nutrients. Bamboo shoots contain protein, amino acids, dietary fiber and various trace elements, and are excellent raw materials for healthy food. Bamboo shoots can not only meet the demands of domestic and foreign markets, but also promote the development of the food processing industry, becoming an important support for increasing farmers' income and regional economy. Some new varieties, such as *Phyllostachys edulis* 'Pachyloen', not only have high yields but also good edible quality, further enhancing economic value (Hu et al., 2020).

2.3 Timber properties and industrial applications

The mechanical properties of *Phyllostachys edulis* timber are excellent, with high strength, light weight and good toughness. It is widely used in industries such as construction, furniture, papermaking and textile (Hu et al., 2020). The cellulose and lignin content of *Phyllostachys edulis* is also very high, making it suitable for the production of high-performance composite materials and biomass energy (Chen et al., 2022). The formation of *Phyllostachys edulis* timber is also regulated by hormones. For instance, gibberellin treatment can promote internode elongation and lignin deposition, thereby enhancing the mechanical properties of timber (Zhang et al., 2018). Due to its large biomass and fast carbon cycle, *Phyllostachys edulis* also has great application potential in carbon sinks and ecological restoration (Hu et al., 2020; Kobayashi et al., 2022).

3 Traditional Breeding Approaches

3.1 Selection of elite germplasm for shoots and timber

The selection of superior germplasm is at the core of traditional bamboo breeding. *Phyllostachys edulis* is widely cultivated because of its high yield of shoots and good quality of timber. Researchers usually select outstanding individual plants or groups by conducting phenotypic observations on natural populations and artificial forests, such as growth rate, bamboo shoot yield, and timber strength, as the basis for production and subsequent breeding. In recent years, the application of whole-genome resequencing and molecular markers has provided genetic data support for these superior traits. These tools help to identify candidate genes related to important traits such as timber mechanical properties, thereby improving germplasm utilization efficiency (Del Giudice et al., 2022).

3.2 Vegetative propagation and clonal breeding

It is rare for *Phyllostachys edulis* to flower and bear fruit, and its generation cycle is very long (generally 60 to 120 years), so asexual reproduction has become the main method of propagation and breeding. *Phyllostachys edulis* mainly expands through underground whip roots and can form large-scale clonal colonies. Studies have found that most of *Phyllostachys edulis* forests in East Asia almost all originated from the same clonal line, and human transplanting and natural expansion jointly created an extremely large single clonal population (Isagi et al., 2015). In addition, tissue culture and cuttings have also been used to rapidly propagate superior strains and ensure the stable transfer of traits (Isagi et al., 2015; Huang et al., 2022a). However, long-term reliance on asexual reproduction has led to very low genetic diversity of *Phyllostachys edulis*, which also increases its risk when facing pests, diseases and environmental stress (Isagi et al., 2015).

3.3 Hybridization attempts and limitations in bamboo breeding

The hybrid breeding of *Phyllostachys edulis* is very difficult. The biggest problem is that its flowering habit is extremely irregular and its seeds are very difficult to obtain (Gao, 2021). Even if it flowers occasionally, the number of seeds is small, the germination rate is low, and the seedlings have difficulty competing with mature bamboo or other tree species in the natural environment. Therefore, it is difficult to form a new dominant population (Isagi et al., 2015; Gao, 2021). At present, traditional hybrid breeding is hardly applicable to *Phyllostachys edulis*, and only natural hybridization that occurs by chance can be relied upon. Some studies have attempted to create new genetic variations by means such as radiation mutagenesis, but they are still limited in practical application, such as the difficulty in obtaining materials and the poor stability of traits (Gao, 2021).

4 Molecular and Genomic Insights

4.1 Genetic resources: genome sequencing and transcriptome studies

Phyllostachys edulis is an important bamboo species that can be used as shoot and timber production. However, due to its extremely long flowering period and the rarity of sexual reproduction, traditional hybrid breeding is difficult to carry out. In recent years, the whole genome sequencing of *Phyllostachys edulis* has been completed, which provides a foundation for molecular breeding and gene editing and greatly expands the available genetic resources (Gao, 2021). Transcriptome analysis revealed that there were many key gene expression changes in *Phyllostachys edulis* at different growth stages, especially during the rapid growth stage of the bamboo shoot. Differentially expressed genes (DEGs) related to hormone signaling, sugar and starch metabolism were identified as a priority. These results provide important clues for studying the growth regulation mechanism and mining genetic resources (Lan et al., 2020; Li et al., 2022).

4.2 Identification of genes linked to shoot yield, nutritional quality, and timber strength

Through transcriptome and small RNA sequencing, researchers identified key genes and miRNAs related to bamboo shoot elongation, lignification and primary thickening. The genes related to bamboo shoot yield and nutrition are mainly concentrated in cell division, hormone signaling and carbon metabolism pathways (Lan et al., 2020; Li et al., 2022). In terms of timber properties, the lignification level of *Phyllostachys edulis* directly determines the performance of the timber. By using the integrated analysis of transcriptome, miRNA and degradation omics, researchers established a regulatory network of miRNA-transcription factor-enzyme genes and found that genes such as *PeLAC20* could significantly increase lignin content, which provided molecular targets for material improvement (Yang et al., 2021; Li et al., 2022). In addition, the AGO family genes have also been proven to play an important role in the tillering and plant type development of bamboo (Yue et al., 2024).

4.3 Marker development for selection of dual-purpose traits

With the in-depth research on genomics and functional genes, molecular marker-assisted selection (MAS) of *Phyllostachys edulis* has become possible. Gene editing tools such as CRISPR/Cas9 and efficient genetic transformation systems have provided new methods for improving target traits (such as high-yield bamboo shoots and high-quality timber) (Huang et al., 2022a). At present, existing studies have combined transcriptome and miRNA analysis to screen out candidate genes and molecular markers related to bamboo shoot traits, laying the foundation for the next step of molecular breeding and rapid selection (Huang et al., 2022a; Li et al., 2022).

5 Breeding Strategies for Shoot Production

5.1 Early sprouting, rapid growth, and yield-related traits

The early growth and rapid growth characteristics of bamboo shoots directly determine their yield and economic value. Transcriptome analysis revealed that during the early and rapid growth stage of bamboo shoots, genes related to cell division, hormone signal transduction (such as the cytokinin pathway), and sugar and starch metabolism were all highly expressed. These genes provide potential targets for molecular marker-assisted selection and genetic engineering breeding (Lan et al., 2020). In addition, studies have shown that the Argonaute family gene (*PhAGO*) can regulate tillers and leaf numbers, thereby affecting the growth rate and external structure of bamboo shoots, which provides a molecular basis for regulating yield and morphology (Yue et al., 2024).

5.2 Nutritional enhancement and flavor-related breeding targets

Bamboo shoots, as food, also focus on breeding for their nutritional value and flavor quality. Studies have found that the expression of genes related to carbohydrate metabolism such as sugar and starch is closely related to energy accumulation and flavor formation (Lan et al., 2020). By using genomic and transcriptomic data, key genes regulating nutritional components can be screened out. Combined with gene editing technology, it is expected to achieve nutritional fortification and flavor improvement (Gao, 2021; Huang et al., 2022a).

5.3 Disease and pest resistance for sustainable shoot production

Pests and diseases are the main problems affecting the yield and quality of bamboo shoots. Molecular breeding and genetic engineering have been employed to screen and validate stress-resistant genes. For instance, studies have found that the CCCH zinc finger protein gene *PeC3H74* can significantly enhance drought resistance and salt tolerance in transgenic plants, indicating its great potential in stress-resistant breeding (Lan et al., 2023a). Meanwhile, the establishment of molecular markers and gene editing platforms has also provided technical support for the rapid acquisition of excellent bamboo shoot varieties resistant to diseases and pests (Gao, 2021; Huang et al., 2022a).

6 Breeding Strategies for Timber Production

6.1 Improving culm strength, density, and mechanical properties

Enhancing the strength and mechanical properties of *Phyllostachys edulis* culms is one of the main goals of timber breeding. Studies have shown that through whole-genome resequencing and association study, some candidate genes related to mechanical traits such as tensile strength have been identified, laying the foundation for molecular marker-assisted selection and precision breeding (Del Giudice et al., 2022). Meanwhile, gene editing technologies such as CRISPR/Cas9 can directly act on the key genes that control cell wall synthesis and lignin accumulation, thereby improving mechanical properties (Gao, 2021; Huang et al., 2022a). These methods have broken through the limitations of long breeding cycles and low efficiency in traditional breeding, and are expected to significantly enhance the utilization value of bamboo in terms of structure.

6.2 Breeding for uniformity in culm size and quality

Phyllostachys edulis itself has significant morphological differences, resulting in inconsistent culm sizes and qualities, which has an impact on industrial utilization. Studies have found that signal transduction and metabolic pathways during bamboo culms growth are related to this difference, among which genes of cell division and hormone signals (such as cytokinin) play an important role (Lan et al., 2020). By using molecular markers, gene editing and clonal selection, superior genotypes can be screened out and trait stability can be maintained, thereby improving the consistency of culms (Gao, 2021). In addition, methods such as radiation mutagenesis can also create new genetic variations and increase the diversity of breeding materials.

6.3 Resistance to biotic and abiotic stresses affecting timber

The production of *Phyllostachys edulis* culms is also often affected by stresses such as pests and diseases, drought and saline-alkali conditions. In recent years, researchers have discovered some genes related to stress resistance, such as *PeC3H74* and *PeLEA14*. These genes can significantly improve the drought resistance and salt tolerance of plants after overexpression (Huang et al., 2022b; Lan et al., 2023a). Transcriptome and functional genomics studies also provide abundant candidate gene resources (Huang et al., 2022b). By regulating these genes through genetic engineering methods, new timber-type *Phyllostachys edulis* varieties with better stress resistance and more stable yield can be cultivated (Huang et al., 2022a; Huang et al., 2022b; Lan et al., 2023a).

7 Case Study: Breeding and Utilization of *P. edulis*

7.1 Breeding program background and objectives

Phyllostachys edulis is one of the most important uniaxial bamboo species in the world and is mainly used in the production of bamboo shoots and bamboo timbers. It has long relied on asexual reproduction and has a long flowering cycle, so its genetic diversity is low. These characteristics have led to slow progress in traditional breeding, making it difficult to meet the industry's demand for high-yield, high-quality and stress-resistant new varieties. In recent years, research has focused on increasing the yield and quality of bamboo shoots, enhancing the strength and toughness of bamboo, as well as improving their stress resistance and adaptability. Meanwhile, new technologies such as molecular assisted breeding and gene editing have gradually been applied to the research of *Phyllostachys edulis* (Isagi et al., 2015; Del Giudice et al., 2022; Huang et al., 2022a; Li et al., 2025).

7.2 Key methodologies applied (clonal selection, molecular tools, field trials)

In actual breeding, clonal selection and asexual reproduction remain the main methods. Since seed propagation is rare, researchers often select outstanding variants (such as *Phyllostachys edulis* 'Pachyloen') through field investigation and trait assessment, and then rapidly propagate them by division or tissue culture methods (Isagi et al., 2015; Hu et al., 2020). With the advancement of genomic research on *Phyllostachys edulis*, tools such as molecular marker-assisted selection (MAS), genome-wide association study (GWAS), transgenic and CRISPR/Cas9 have gradually been introduced into breeding to verify key genes and conduct targeted improvement (Figure 2) (Lan et al., 2020; Del Giudice et al., 2022; Huang et al., 2022a). Furthermore, multi-point field trials can help evaluate the growth, yield, stress resistance and timber properties of candidate strains, thereby ensuring the stability and application prospects of new varieties in different environments (Zhao et al., 2016; Hu et al., 2020; Del Giudice et al., 2022).

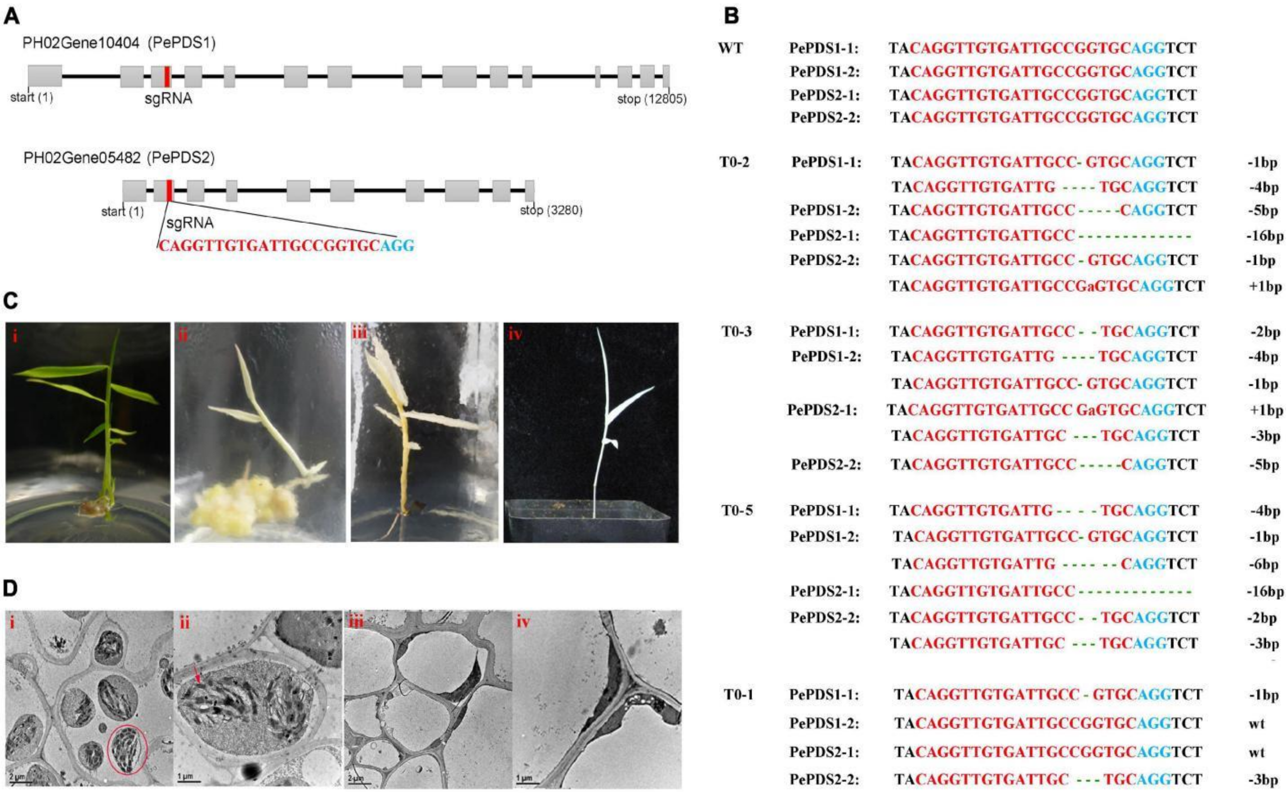

Figure 2 Genome editing of *PePDS* gene by CRISPR/Cas9 (Adopted from Huang et al., 2022a)

Image caption: (A) Genome structures of *PePDS1* and *PePDS2*. Gray boxes, exons; black line, intron; red rectangle, sgRNA target site; red letters, sgRNA target regions; blue letters, PAM regions. (B) Mutations at sgRNA site of putative homozygous *pds1pds2* lines (T0-2, T0-3, and T0-5) and a representative of heterozygous mutant (T0-1). Green lowercase letters, base insertions; dotted lines, base deletions. (C) Albino shoots and regenerated plant of homozygous *pds1pds2* mutant (ii-iv). i, wild type. (D) Transmission electron microscope observation of leaves. i and ii, wild type. iii and iv, albino mutant. Red circle, chloroplasts; red arrow, thylakoid lamellae (Adopted from Huang et al., 2022a)

7.3 Outcomes: improved varieties and their adoption in bamboo industries

The promotion of superior varieties is of great significance to the development of *Phyllostachys edulis* industry. For instance, *Phyllostachys edulis* 'Pachyloen' has thicker walls and higher biomass, and also possesses the characteristics of high-quality bamboo shoots and timber. It has been widely applied in southern China, significantly enhancing economic benefits (Isagi et al., 2015; Hu et al., 2020). On this basis, molecular breeding has brought about new impetus for development. Based on genomic and molecular marker studies, some genes related to timber strength, stress resistance and bamboo shoot yield have been screened out, providing a basis for targeted improvement (Lan et al., 2020; Del Giudice et al., 2022; Huang et al., 2022a). These improved varieties have not only promoted the upgrading of the bamboo shoot and timber industry, increased resource utilization and farmers' income, but also provided support for the sustainable management of bamboo forests (Isagi et al., 2015; Hu et al., 2020; Del Giudice et al., 2022).

8 Challenges and Limitations

8.1 Long breeding cycles and limitations in sexual reproduction

The flowering of *Phyllostachys edulis* is very rare and has no fixed pattern. The sexual reproduction cycle often takes 60 to 120 years, or even longer, to complete once. This makes traditional hybrid breeding almost impossible to carry out, and the acquisition of new germplasm and the recombination of superior traits are also very difficult. In addition, in the wild, *Phyllostachys edulis* mainly relies on asexual reproduction. Natural renewal lacks diversity and the genetic basis is relatively narrow, which further increases the difficulty of breeding (Isagi et al., 2015; Gao, 2021).

8.2 Technical gaps in functional genomics and marker deployment

Although some achievements have been made in the genomic and transcriptomic research of *Phyllostachys edulis* in recent years, its large genome, polyploid characteristics, and complex genetic background all pose challenges to functional genomics research and the development of molecular markers. *Phyllostachys edulis* lacks an efficient genetic transformation system, which leads to the slow progress of gene function verification and molecular breeding. There have been initial attempts at gene editing methods such as CRISPR/Cas9, but their transformation efficiency is not high and they are highly dependent on genotypes. Meanwhile, the application of molecular markers in actual breeding is not yet mature enough to achieve precise improvement of complex traits (Zhao et al., 2016; Del Giudice et al., 2022; Huang et al., 2022a).

8.3 Trade-offs between shoot yield and timber quality

Phyllostachys edulis is both a crop for bamboo shoots and a bamboo species for timber, but there is a clear contradiction between the yield of bamboo shoots and the quality of timer. When the yield of bamboo shoots is increased, the growth cycle will be shortened, the degree of lignification will decline, and the performance of the timer will decrease accordingly. If high-quality timber is pursued, the yield and quality of bamboo shoots may be lost. Studies on molecular regulatory networks have shown that genes regulating lignin synthesis and cell wall development interact with pathways such as hormone signaling and carbon metabolism that control bamboo shoot growth, making it more difficult to simultaneously improve the two types of traits (Shou et al., 2019; Lan et al., 2020; Yang et al., 2021).

9 Future Perspectives

9.1 Multi-omics integration for trait dissection and breeding efficiency

The integration of multi-omics data (genomic, transcriptomic, proteomic and metabolomic) provides new opportunities for the study of complex traits in bamboo. Through these data, the key genes and regulatory networks related to bamboo shoot yield, timer quality and stress resistance can be systematically analyzed and located. This method helps accelerate the screening of functional genes and the development of molecular markers, thereby promoting the progress of molecular breeding. Previous studies have screened out the transcription factor PhebZIP47 related to drought resistance using the transcriptome, and confirmed its role in stress resistance through co-expression networks and functional verification, providing a scientific basis for molecular breeding (Lan et al., 2023b). In the future, the combination of multi-omics big data and artificial intelligence will further improve trait analysis and breeding efficiency (Gao, 2021; Lan et al., 2023b).

9.2 Application of CRISPR and advanced biotechnological tools

The development of gene editing technologies such as CRISPR/Cas9 has also provided new tools for the precise improvement of bamboo. The latest research has established an efficient *Phyllostachys edulis* transformation and CRISPR/Cas9 system, achieving site-directed mutagenesis and functional verification of target genes, providing a basis for molecular breeding and new germplasm cultivation (Huang et al., 2022a). By optimizing the design and transformation conditions of sgRNA, the efficiency of gene editing has been greatly enhanced. In the future, this technology can be applied to the improvement of important traits such as yield, quality and stress resistance. Combining high-throughput detection and label-free editing strategies can further accelerate the breeding of new varieties (Gao, 2021; Huang et al., 2022a).

9.3 Developing climate-resilient and high-value bamboo cultivars

In the face of climate change and diverse market demands, it is particularly important to cultivate new varieties of *Phyllostachys edulis* that are high-yielding, high-quality, stress-resistant and have high added value. Researchers can screen out gene resources that are drought-resistant, cold-resistant and disease-resistant through molecular methods combined with traditional breeding to enhance the climate adaptability of *Phyllostachys edulis* (Lan et al., 2023b). Meanwhile, high-value bamboo species containing functional components that can be used in multiple industries such as food, building materials and medicine can also be developed to expand the industrial chain and improve economic and ecological benefits (Gao, 2021; Lan et al., 2023b). In the future, the combination of molecular marker-assisted selection, gene editing and multi-omics integration will drive *Phyllostachys edulis* breeding towards intelligence and efficiency (Gao, 2021; Huang et al., 2022a; Lan et al., 2023b).

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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