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DEP1 and Panicle Architecture: Influencing Rice Yield through Genetic Modulation

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Abstract In recent years, with the rapid development of molecular biology and genomics, it has become possible to improve rice panicle architecture through gene regulation techniques, thereby enhancing yield. The *DEP1* (Dense and Erect Panicle 1) gene, an important gene influencing rice panicle morphology and yield, provides new perspectives and approaches for rice genetic improvement. This study explores the functional mechanisms of the *DEP1* gene, elucidates how it regulates rice panicle architecture, and assesses its impact on yield. Through case studies in molecular biology, genomics, and field trials, we conducted an in-depth analysis of the genetic variation, molecular mechanisms, and performance of the *DEP1* gene under different environments. The research findings indicate that optimizing the *DEP1* gene can significantly improve panicle architecture and increase yield. By unraveling the genetic regulatory network of the *DEP1* gene, this study not only contributes to understanding the genetic basis of rice panicle development but also offers new strategies and targets for rice molecular breeding. This is crucial for advancing rice breeding technology and ensuring global food security.

Keywords Rice (*Oryza sativa* L.); *DEP1* gene; Gene regulation; Yield enhancement; Molecular breeding

1 Introduction

Rice (*Oryza sativa* L.) is a staple food for more than half of the world's population, making its yield a critical factor in global food security. Among the various genetic and agronomic traits influencing rice yield, panicle architecture plays a pivotal role. The panicle, which is the flowering head of the rice plant, directly impacts the number of grains produced per plant (Zhu et al., 2013; Park et al., 2018; Sowmya et al., 2023). Recent advances in genetic research have identified several key genes that regulate panicle architecture, with the *DENSE AND ERECT PANICLE 1* (*DEP1*) gene emerging as a significant contributor to yield enhancement (Piao et al., 2009).

Panicle architecture, characterized by the morphology, number, and length of primary and secondary branches, is a crucial determinant of grain yield in rice. Variations in these traits can lead to significant differences in the number of grains per panicle and overall plant productivity. For instance, the dense and erect panicle (EP) phenotype, which is associated with a higher number of grains per panicle and improved lodging resistance, has been a target for rice breeding programs aiming to increase yield (Huang et al., 2009; Qiao et al., 2011; Xu et al., 2016). The EP phenotype not only enhances grain yield but also contributes to better nitrogen use efficiency and stress tolerance, making it a valuable trait for sustainable rice production (Xu et al., 2016; Zhao et al., 2019).

The *DEP1* gene, which encodes a G protein γ subunit, has been identified as a key regulator of panicle architecture in rice. The dominant allele of DEP1 results in a gain-of-function mutation that enhances meristematic activity, leading to a reduced length of the inflorescence internode and an increased number of grains per panicle (Huang et al., 2009). This mutation is common in many high-yielding rice varieties and has been widely utilized in rice breeding programs (Huang et al., 2009; Xu et al., 2016). Additionally, *DEP1* is involved in regulating the carbon-nitrogen metabolic balance, which affects both grain yield and quality (Zhao et al., 2019). Variations in the *DEP1* gene contribute to the diversity of panicle traits observed in different rice varieties, further underscoring its importance in rice genetics and breeding (Zhao et al., 2016).

This study delves into the specific impact of the *DEP1* gene on rice panicle architecture and yield. By employing molecular biology techniques, we elucidate the functional mechanisms of the *DEP1* gene, clarifying its role and regulatory network in the development of rice panicles. Additionally, we assess the practical effects of *DEP1* gene variation on panicle morphology and yield, providing scientific basis and technical support for rice molecular breeding, thereby promoting further enhancement of rice yield.

2 *DEP1* Gene: Functions and Mechanisms

2.1 Discovery and characterization of the *DEP1* gene

The *DEP1* locus was identified as a major quantitative trait locus (QTL) influencing grain yield through the modulation of panicle architecture. The dominant allele at the *DEP1* locus is a gain-of-function mutation that results in the truncation of a phosphatidylethanolamine-binding protein-like domain protein. This mutation enhances meristematic activity, leading to a reduced length of the inflorescence internode, an increased number of grains per panicle, and consequently, a higher grain yield. This allele is prevalent in many high-yielding Chinese rice varieties and is believed to have been introduced relatively recently into the cultivated rice gene pool (Huang et al., 2009).

Further studies have shown that the *DEP1* gene is highly expressed in young tissues, particularly in young panicles, indicating its crucial role during the early stages of panicle development. The mutation in *DEP1* primarily affects the rapid elongation of the rachis and primary and secondary branches, without impairing the initiation or formation of panicle primordia. This results in a more compact plant type, which is advantageous for achieving higher yields without significant alterations in grain production (Li et al., 2010).

The *DEP1* gene's role extends beyond individual plant yield to population-level improvements. The erect panicle architecture conferred by the *DEP1* allele optimizes canopy structure, allowing more light to penetrate the lower leaves, thereby enhancing photosynthetic efficiency and biomass accumulation. This trait also enables higher planting densities and better resource utilization, contributing to sustainable agricultural practices (Fei et al., 2019).

2.2 Molecular mechanisms: how *DEP1* affects panicle development

The *DENSE AND ERECT PANICLE 1* (*DEP1*) gene plays a crucial role in determining the architecture of the rice panicle, which directly impacts grain yield. *DEP1* encodes a protein with a phosphatidylethanolamine-binding protein-like domain, and a gain-of-function mutation in this gene results in a truncated protein that enhances meristematic activity. This increased activity leads to a reduced length of the inflorescence internode, an increased number of grains per panicle, and consequently, a higher grain yield (Huang et al., 2009).

Additionally, *DEP1* is involved in regulating the carbon-nitrogen metabolic balance, which affects grain yield and quality. Overexpression of *DEP1* enhances nitrogen uptake and assimilation, although it disrupts the carbon-nitrogen balance, leading to increased grain numbers per panicle but decreased grain quality (Zhao et al., 2019). The *DEP1* gene also interacts with the G protein signaling pathway, influencing various physiological and morphological functions, including nitrogen uptake and stress tolerance (Xu et al., 2016).

2.3 Variants of *DEP1* and their impacts on rice phenotypes

Several variants of the *DEP1* gene have been identified, each with distinct impacts on rice phenotypes. The dominant allele of *DEP1*, which is a gain-of-function mutation, is common in many high-yielding Chinese rice varieties and has been shown to enhance grain yield by increasing the number of grains per panicle (Huang et al., 2009). Another study identified a novel dense and erect panicle (EP) mutant, dep3, which is controlled by a single recessive gene. The dep3 mutant exhibits a denser and more erect panicle architecture, with more small vascular bundles and a thicker culm, contributing to its unique phenotype (Qiao et al., 2011).

Furthermore, the *DEP1* gene has been linked to improved nitrogen use efficiency and lodging tolerance, making it a valuable target for rice breeding programs aimed at developing high-yielding and stress-tolerant varieties (Xu et al., 2016). The *DEP2* gene, another variant affecting panicle architecture, primarily influences the elongation of rachis and primary and secondary branches, resulting in a dense and erect panicle phenotype without significantly altering grain production (Li et al., 2010). These findings highlight the diverse roles of *DEP1* and its variants in modulating panicle architecture and grain yield in rice.

3 Genetic Modulation of *DEP1*

3.1 Techniques for modulating *DEP1* expression

The genetic modulation of the *DENSE AND ERECT PANICLE 1* (*DEP1*) gene has been a focal point in rice breeding due to its significant impact on panicle architecture and grain yield. Various techniques have been employed to modulate *DEP1* expression, including natural variation, induced mutations, and gene editing. Natural variation at the *DEP1* locus has been a key source of genetic diversity. A dominant allele at the *DEP1* locus, which is a gain-of-function mutation, has been identified to enhance meristematic activity, leading to a reduced length of the inflorescence internode and an increased number of grains per panicle (Huang et al., 2009). This allele is prevalent in many high-yielding Chinese rice varieties and has also been found in temperate cereals, indicating its evolutionary significance.

Induced mutations have also been utilized to study and exploit *DEP1*. For instance, the dep3 mutant, derived from the Japonica cultivar Hwacheong treated with N-methyl-N-nitrosourea, exhibits a dense and erect panicle phenotype. The DEP3 gene, identified through map-based cloning, encodes a patatin-like phospholipase A2 (PLA2) superfamily domain-containing protein, and the mutation involves a 408 bp genomic deletion (Qiao et al., 2011). Gene editing technologies, such as CRISPR/Cas9, have provided precise tools for modulating *DEP1*. A study demonstrated the use of CRISPR/Cas9 to create an erect panicle mutant at the *DEP1* locus, which resulted in improved canopy structure and increased biomass under low fertilization conditions (Fei et al., 2019). This approach not only elucidates the functional role of *DEP1* but also offers practical applications in sustainable agriculture.

3.2 Impacts of genetic alterations of *DEP1* on rice yield

Genetic alterations of *DEP1* have profound impacts on rice yield, primarily through modifications in panicle architecture. The gain-of-function mutation at the *DEP1* locus enhances grain yield by increasing the number of grains per panicle. This mutation is associated with a reduced length of the inflorescence internode and increased meristematic activity, which collectively contributes to higher grain production (Huang et al., 2009). The dep3 mutant, characterized by a dense and erect panicle, also shows significant changes in panicle traits, including panicle length, grain shape, and grain number per panicle. The mutation leads to more small vascular bundles and a thicker culm, which support the erect panicle phenotype and potentially enhance yield stability (Qiao et al., 2011).

However, not all genetic alterations of *DEP1* result in positive yield outcomes. For example, the introgression of the qPE9-1 allele, which confers panicle erectness, has been shown to decrease grain yield per plant by 30% in some japonica rice varieties. This reduction is attributed to decreased panicle length, plant height, and 1000-grain weight, highlighting the pleiotropic effects of *DEP1* and the need for careful selection of complementary genes in breeding programs (Yi et al., 2011). Furthermore, the combination of *DEP1* with other yield-related genes, such as IPA1, has been explored to optimize yield components. Studies have shown that the *DEP1* and ipa1 alleles can offset each other’s negative effects, leading to an ideal plant type with improved yield potential (Xu et al., 2014). This synergistic approach underscores the importance of integrating multiple genetic factors to achieve desirable agronomic traits.

3.3 Field results of *DEP1* modulation

Several studies have demonstrated the impact of *DEP1* modulation on rice yield through field trials. For instance, the introduction of the dominant *DEP1* allele into various rice cultivars has consistently resulted in increased grain yield due to enhanced panicle architecture. The gain-of-function mutation in *DEP1* leads to a higher number of grains per panicle, which directly translates to increased yield (Huang et al., 2009).

In another study, the *dense and erect panicle 3* (*DEP3*) mutant, derived from the *Oryza sativa* ssp. *japonica* cultivar Hwacheong, exhibited a similar phenotype with erect panicles and increased grain number per panicle. The DEP3 gene, identified as a patatin-like phospholipase A2 (PLA2) superfamily domain-containing protein, plays a significant role in the formation of vascular bundles, contributing to the dense and erect panicle phenotype. This mutation provides another valuable resource for rice breeding programs aimed at improving yield (Qiao et al., 2011).

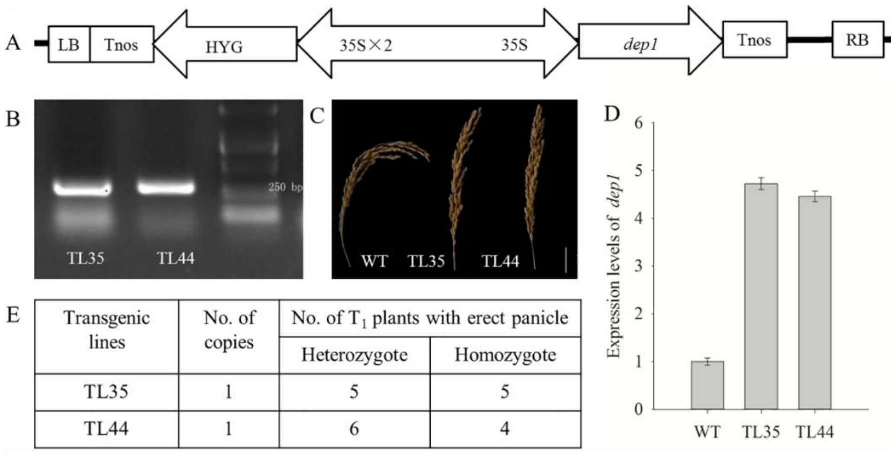
Furthermore, the *CLUSTERED PRIMARY BRANCH 1* (*CPB1*) gene, a new allele of DWARF11 (D11), has been shown to control panicle architecture and seed size. Overexpression of CPB1/D11 in rice plants resulted in larger seed size and enhanced grain yield without negatively affecting other agronomic traits. This demonstrates the potential of manipulating CPB1/D11 expression to improve rice yield through genetic modulation (Wu et al., 2016). The *Short Panicle 3* (*SP3*) gene, encoding a DNA binding with one finger (Dof) transcriptional activator, also influences panicle architecture by modulating cytokinin homeostasis. Knockdown mutations in *SP3* lead to smaller panicles with fewer branches and spikelets, highlighting the importance of *SP3* in regulating panicle development and grain yield (Huang et al., 2019).

4 Case Studies: *DEP1* and Rice Yield Enhancement

4.1 Analysis of *DEP1* gene manipulation experiments

Due to the significant impact of the *DEP1* gene on panicle architecture, it has become a focal point for enhancing rice yield. The dominant allele at the *DEP1* locus is a gain-of-function mutation that enhances meristematic activity, leading to a reduced length of the inflorescence internode and an increased number of grains per panicle, thereby boosting rice yield. This allele is prevalent in many high-yielding Chinese rice varieties and is a relatively recent addition to the cultivated rice gene pool (Huang et al., 2009). Additionally, the use of CRISPR/Cas9 gene editing technology to edit the *DEP1* locus has been shown to improve canopy structure, allowing more light to reach the leaves below the panicle, thereby increasing biomass and yield under low-fertilizer conditions (Fei et al., 2019).

Huang et al. (2018) studied the use of CRISPR/Cas9 technology to edit the *DEP1* gene, resulting in multiple mutants that exhibited an increased number of grains per panicle and overall yield improvement (Huang et al., 2018). Zhao et al. (2019) demonstrated that genome editing-induced mutagenesis can develop superior *DEP1* gene alleles (Figure 1), further enhancing grain yield under controlled conditions.



Transgenic lines	No. of copies	No. of T_1 plants with erect panicle	
		Heterozygote	Homozygote
TL35	1	5	5
TL44	1	6	4

Figure 1 Generation of *DEP1* overexpressed plants (Adopted from Zhao et al., 2019)

Image caption: (A) The construct of the plasmid containing the CaMV 35S promoter (35S), *DEP1* and the terminator (Tnos) between the right (RB) and the left (LB) borders of the T-DNA. The hygromycin resistance gene (HYG) was located between the LB and the 35S promoter. (B) Identification of positive transgenic plants in T0 generation by PCR. (C) Panicle architecture for wildtype and transgenic T0 plants. (D) Expression levels of *DEP1* in transgenic T0 plants. Expression levels relative to wildtype plants set to be one. Data shown as means ± SD (n = 3). (E) Identification of copy numbers in transgenic T0 plants and homozygote in transgenic T1 plants by quantitative real-time PCR (Adopted from Zhao et al., 2019)

Zhao et al. (2019) analyzed the generation process and phenotype of transgenic rice plants overexpressing the *DEP1* gene. The study found differences in panicle architecture between wild-type (WT) and transgenic plants (TL35 and TL44), with the transgenic plants exhibiting more erect panicles. Additionally, the expression levels of the *DEP1* gene were significantly higher in TL35 and TL44 compared to the wild type. These results indicate that overexpression of the *DEP1* gene through genome editing can significantly alter panicle architecture and potentially increase rice yield. This provides new insights and methods for optimizing rice cultivation using genome editing technology.

4.2 Success stories: implementations and outcomes in different environments

The manipulation of the *DEP1* gene has yielded positive results across various environments. For instance, CRISPR-dep1 mutants demonstrated higher yield under low fertilization conditions compared to wild-type plants under high fertilization, indicating its potential for sustainable agricultural practices (Fei et al., 2019). Zhao et al. (2016) introduced the *DEP1* allele into high-yielding japonica rice varieties in northern China, resulting in diverse panicle traits with significant improvements in the number of primary and secondary branches and grain number per panicle (Zhao et al., 2016). These findings underscore the diversity and effectiveness of *DEP1* gene manipulation in different environmental contexts.

In China, the widespread adoption of high-yielding rice varieties containing the *DEP1* allele has led to increased grain yield and improved nitrogen use efficiency. This allele has played a crucial role in developing rice varieties that maintain high yields even under low nitrogen conditions, which is essential for sustainable agriculture (Sun et al., 2014). Additionally, combining *DEP1* with other yield-related genes, such as Gn1a, has resulted in the cultivation of rice varieties that are both high-yielding and of high quality, demonstrating the versatility and effectiveness of this gene in different agricultural environments (Wu et al., 2022).

4.3 Comparative analysis with traditional breeding techniques

Compared to traditional breeding techniques, the genetic manipulation of the *DEP1* gene offers more precise and rapid improvements in rice yield. While traditional breeding methods are effective, they often require multiple generations to achieve the desired traits. In contrast, gene editing techniques like CRISPR/Cas9 allow for targeted modifications, leading to immediate and significant enhancements in panicle architecture and yield (Fei et al., 2019). Studies have shown that the yield improvements obtained through *DEP1* gene editing are significantly higher and more consistent than those achieved through traditional breeding methods (Xu et al., 2016). Additionally, the use of genetic tools enables the stacking of multiple beneficial traits, which is difficult to achieve solely through traditional methods (Li et al., 2016). The genetic diversity introduced through *DEP1* manipulation, as seen in high-yielding japonica rice varieties, provides a broader genetic base for future breeding programs (Zhao et al., 2016). This contrasts with the narrower genetic diversity typically seen in traditional breeding, which can limit the potential for further improvements.

5 Advances in Genomic Technologies for Studying *DEP1*

5.1 Next-generation sequencing and its role in *DEP1* research

Next-generation sequencing (NGS) has revolutionized the study of genetic loci such as *DEP1* by enabling high-throughput and precise identification of genetic variations. For instance, the identification of 45 SNPs and 26 indels within the *DEP1* locus in a collection of high-yielding japonica rice varieties was made possible through NGS technologies. This detailed genetic mapping has provided insights into the genetic diversity of *DEP1* and its contribution to panicle traits, such as the number of primary and secondary branches and grain number per panicle (Zhao et al., 2016). Additionally, NGS has facilitated the fine mapping and candidate gene analysis of other related genes, such as *DEP3*, which also influence panicle architecture and yield (Qiao et al., 2011).

Methods such as MutMap and MutMap+ utilize NGS to quickly identify key nucleotide changes in rice mutants by performing whole-genome resequencing of the DNA from mutant progeny. This is crucial for understanding the functional genetic basis of *DEP1* (Fekih et al., 2013). These methods allow researchers to directly associate phenotypic variations with genomic data, thereby enhancing the precision of genetic studies.

5.2 Use of CRISPR/Cas9 for precise *DEP1* modification

CRISPR/Cas9 technology has emerged as a powerful tool for precise genetic modifications, including those at the *DEP1* locus. This technology has been employed to create erect panicle mutants by editing the *DEP1* gene, resulting in improved canopy structure and increased yield. For example, a CRISPR/Cas9-edited *DEP1* mutant exhibited a more efficient canopy structure, allowing more light to reach the leaves under the panicle, which in turn enhanced biomass and yield under low fertilization conditions (Fei et al., 2019). Furthermore, CRISPR/Cas9 has been used to develop near-isogenic lines (NILs) with modified grain shape genes in the background of erect-panicle geng/japonica rice, demonstrating the potential of this technology to improve both yield and grain quality (Mao et al., 2021).

5.3 Integrating genomic data for enhanced breeding strategies

The integration of genomic data into breeding strategies has significantly enhanced the efficiency and effectiveness of rice breeding programs. By combining genomic information with traditional breeding techniques, researchers have been able to develop high-yielding rice varieties with desirable traits (Grenier et al., 2015; Cui et al., 2019). For instance, the identification of a dominant allele at the *DEP1* locus, which enhances meristematic activity and increases grain yield, has been instrumental in breeding high-yielding rice varieties in China (Huang et al., 2009). Additionally, the integration of genomic data has facilitated the development of new plant types with improved yield potential, such as the pyramiding of high-yielding npt1 and *DEP1*-1 alleles (Wang et al., 2017). This approach not only improves individual plant yield but also optimizes population structure for better light penetration and resource use efficiency (Fei et al., 2019).

In summary, advances in genomic technologies, including NGS and CRISPR/Cas9, have significantly contributed to the understanding and manipulation of the *DEP1* locus. These technologies have enabled precise genetic modifications and the integration of genomic data into breeding strategies, leading to the development of high-yielding rice varieties with improved panicle architecture and overall yield.

6 Breeding Strategies Incorporating *DEP1*

6.1 From gene to field: translating *DEP1* research into practical applications

The *dense and erect panicle 1* (*DEP1*) gene has been a focal point in rice breeding due to its significant impact on grain yield and panicle architecture. The *DEP1* gene, which encodes a phosphatidylethanolamine-binding protein-like domain protein, enhances meristematic activity, leading to a reduced length of the inflorescence internode and an increased number of grains per panicle (Huang et al., 2009). This gene has been widely utilized in Chinese high-yielding rice varieties, demonstrating its practical application in breeding programs aimed at increasing rice yield.

The application of *DEP1* in breeding programs has also been explored through the creation of near-isogenic lines (NILs) using CRISPR/Cas9 technology. These NILs have shown improvements in grain appearance and yield components, indicating that pyramiding *DEP1* with other major-effect grain shape alleles can enhance both yield and quality (Mao et al., 2021). Additionally, the integration of *DEP1* with other yield-related genes, such as IPA1, has been studied to develop hybrid japonica rice with ideal plant types, further demonstrating the practical applications of *DEP1* in breeding programs (Xu et al., 2014).

6.2 Challenges in *DEP1*-based breeding programs

Despite the promising results, there are several challenges associated with *DEP1*-based breeding programs. One major challenge is the narrow genetic diversity of *DEP1*, which limits the potential for further improvements in panicle traits. Studies have shown that the genetic diversity of *DEP1* in high-yielding japonica rice varieties is limited, necessitating efforts to broaden the genetic base for more flexible applications in breeding (Zhao et al., 2016).

Another challenge is the trade-off between yield and grain quality. While the *DEP1* gene contributes to higher yield, it can also negatively impact grain quality, such as grain shape and taste. For instance, the introgression of the qPE9-1 allele, which confers panicle erectness, has been associated with a decrease in grain yield per plant, highlighting the need for careful consideration of the genetic background when incorporating *DEP1* into breeding programs (Yi et al., 2011). Additionally, the erect panicle architecture, while beneficial for yield, can lead to increased chalkiness in grains, which is less desirable in the market (Mao et al., 2021).

6.3 Future prospects for breeding programs focusing on *DEP1*

The future of *DEP1*-based breeding programs lies in addressing the current challenges and leveraging new technologies to enhance both yield and quality. One promising approach is the use of advanced genetic tools, such as CRISPR/Cas9, to create precise modifications in the *DEP1* gene and its associated pathways. This can help in developing rice varieties with optimized panicle architecture and improved grain quality (Mao et al., 2021).

Furthermore, integrating *DEP1* with other beneficial genes, such as those involved in nitrogen use efficiency and lodging resistance, can lead to the development of rice varieties that are not only high-yielding but also resilient to environmental stresses (Zhao et al., 2017). The combination of *DEP1* with genes that enhance canopy structure and light penetration can further improve the overall productivity of rice populations (Fei et al., 2019).

In conclusion, while there are challenges in *DEP1*-based breeding programs, the potential benefits in terms of yield and quality make it a valuable target for future research and development. By addressing the genetic diversity and quality trade-offs, and utilizing advanced genetic tools, breeding programs can continue to make significant strides in improving rice production.

7 Impact of *DEP1* Research on Rice Agriculture

7.1 Enhancements in grain yield and quality

Research on the *DEP1* locus has significantly contributed to the enhancement of grain yield and quality in rice. The dominant allele at the *DEP1* locus, a gain-of-function mutation, has been shown to increase meristematic activity, resulting in a reduced length of the inflorescence internode and an increased number of grains per panicle, thereby boosting grain yield (Huang et al., 2009). This allele is prevalent in many high-yielding Chinese rice varieties and has been a key factor in their success. Additionally, variations in the *DEP1* gene have been linked to the diversity of panicle traits in high-yielding japonica rice varieties, further emphasizing its role in improving rice yield (Zhao et al., 2016). The integration of *DEP1* with other grain shape genes has also been explored to enhance both yield and appearance quality, demonstrating the gene's versatility in rice breeding programs (Figure 2) (Mao et al., 2021).

Mao et al. (2021) studied the comparison of grain shape and related impact factors between YF47dep1 (WT) and near-isogenic lines (NILs). The results showed that the *DEP1* gene significantly affects grain length and width, with significantly increased levels of IAA and BR in the NILs. These findings indicate that the overexpression of the *DEP1* gene significantly impacts rice grain shape, cell structure, and hormone levels, thereby enhancing rice yield and quality. This study reveals the potential of the *DEP1* gene in rice breeding, providing new insights for improving rice production.

7.2 Implications for global rice production and food security

The advancements in understanding and utilizing the *DEP1* locus have profound implications for global rice production and food security. By increasing the grain yield per plant, *DEP1*-enhanced varieties can contribute to higher overall rice production, which is crucial for meeting the food demands of a growing global population. The introduction of *DEP1* into various rice cultivars has shown promise in improving yield potential, which is essential for food security, especially in regions heavily dependent on rice as a staple food (Huang et al., 2009; Zhao et al., 2016). Furthermore, the ability to combine *DEP1* with other high-yielding alleles, such as those affecting panicle architecture and seed size, offers a strategic approach to developing rice varieties that can sustain higher productivity under diverse agricultural conditions (Miura et al., 2010; Wang et al., 2017).

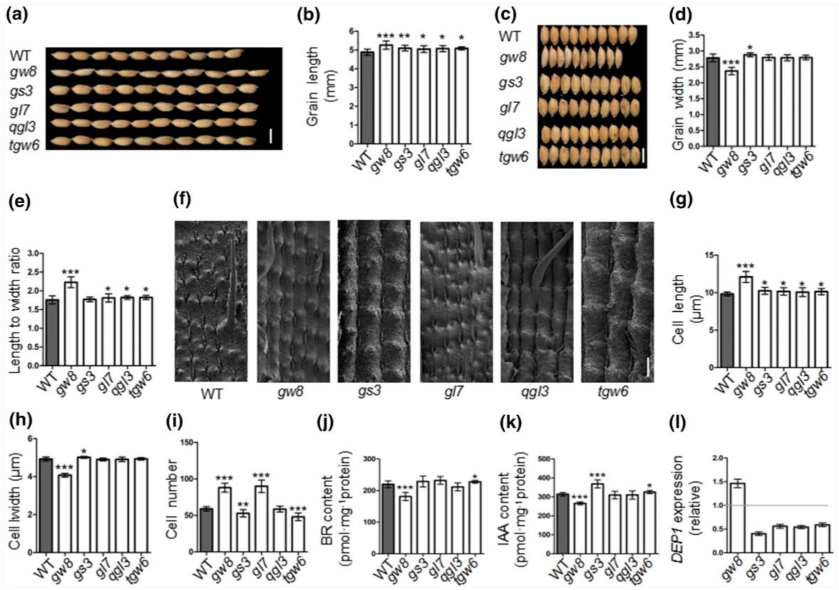


Figure 2 The appearance and determination of grain shape and related impact factors analysis in YF47dep1 (WT) and the NILs (Adopted from Mao et al., 2021)

Image caption: a, b: The appearance (a) and comparison (b) of grain length in WT and NILs. Scale bar = 5 mm, The data represent the mean ± sd, $***P < 0.001$, $**P < 0.01$, $*P < 0.05$; c, d: The appearance (c) and comparison (d) of grain width in WT and NILs. Scale bar = 5 mm; e: The comparison of length to width ratio in WT and NILs; f-i: The appearance (f) and comparison of cell length (j), cell width (h) and number of cells (i) on the outer surface of the glumes in WT and the NILs. Scale bar = 10 μm; j, k: The comparison of IAA (j) and BR (k) levels in YF47dep1 (WT) and the NILs; l: The relative expression of *DEP1* in the NILs (Adopted from Mao et al., 2021)

7.3 Strategies for wider adoption of *DEP1*-enhanced varieties

To maximize the benefits of *DEP1*-enhanced rice varieties, several strategies can be employed for their wider adoption. First, breeding programs should focus on incorporating *DEP1* into a broad range of rice cultivars, including those adapted to different climatic and soil conditions. Marker-assisted selection can facilitate the efficient introgression of *DEP1* into elite cultivars, ensuring that the beneficial traits are retained while maintaining other desirable agronomic characteristics (Zhao et al., 2015). Additionally, educating farmers about the advantages of *DEP1*-enhanced varieties and providing them with access to high-quality seeds can promote adoption at the grassroots level. Collaborative efforts between researchers, agricultural extension services, and policymakers are essential to support the dissemination and sustainable cultivation of these high-yielding varieties (Huang et al., 2009; Zhao et al., 2016). Finally, ongoing research to further understand the genetic and molecular mechanisms of *DEP1* and its interaction with other yield-related genes will continue to drive innovations in rice breeding, ensuring that *DEP1*-enhanced varieties remain at the forefront of efforts to improve rice production and food security globally (Miura et al., 2010; Mao et al., 2021).

8 Future Research Directions

8.1 Unexplored areas in *DEP1* research

Despite significant advancements in understanding the role of the *DEP1* locus in rice yield, several areas remain underexplored. One such area is the detailed molecular mechanism by which *DEP1* influences meristematic activity and panicle architecture. While it is known that the dominant allele at the *DEP1* locus enhances meristematic activity, resulting in a reduced length of the inflorescence internode and an increased number of grains per panicle (Huang et al., 2009), the precise biochemical pathways and interactions with other genetic factors are not fully understood. Additionally, the impact of *DEP1* on other agronomic traits such as disease resistance and stress tolerance warrants further investigation. Understanding these interactions could provide a more holistic approach to rice breeding programs.

8.2 Potential for integrating *DEP1* insights with other genetic research

Integrating insights from *DEP1* research with other genetic studies could lead to more comprehensive strategies for improving rice yield. For instance, combining *DEP1* with other loci such as DEP3, which also influences panicle architecture and grain yield (Qiao et al., 2011), could result in synergistic effects. Moreover, the use of advanced techniques like genome-phenome wide association studies (GPWAS) and genome-wide association studies (GWAS) has identified multiple QTLs and candidate genes related to panicle architecture (Rebolledo et al., 2016; Zhong et al., 2021). These findings could be integrated with *DEP1* research to develop multi-gene approaches for yield improvement. Additionally, the interaction between *DEP1* and other key genes like OsSHI1, which modulates the transcriptional activity of IPA1 and influences plant architecture (Duan et al., 2019), could be explored to optimize plant traits further.

8.3 Prospects for global collaboration in rice genetic research

Global collaboration is essential for advancing rice genetic research and addressing food security challenges. Collaborative efforts can facilitate the sharing of genetic resources, such as diverse rice germplasm collections, which are crucial for studying the genetic diversity of *DEP1* and other loci (Zhao et al., 2016). International research consortia can also promote the standardization of phenotyping and genotyping methods, enabling more robust and comparable results across different studies. Furthermore, collaborative projects can leverage advanced technologies like CRISPR/Cas9 for precise genetic modifications, as demonstrated in studies optimizing canopy structure through *DEP1* gene editing (Fei et al., 2019). By fostering global partnerships, researchers can accelerate the development of high-yielding, resilient rice varieties that can meet the demands of a growing population. By integrating resources and knowledge, researchers can solve larger and more complex problems, such as the adaptability of *DEP1* enhanced rice varieties to different environmental conditions and their performance in different agricultural systems (Hirochika et al., 2004).

9 Concluding Remarks

The *DEP1* (Dense and Erect Panicle 1) gene plays a crucial role in enhancing rice yield by modulating panicle architecture. The dominant allele at the *DEP1* locus is a gain-of-function mutation that results in a truncated phosphatidylethanolamine-binding protein-like domain protein. This mutation enhances meristematic activity, leading to a reduced length of the inflorescence internode, an increased number of grains per panicle, and consequently, a higher grain yield. This allele is prevalent in many high-yielding Chinese rice varieties and has likely been introduced relatively recently into the cultivated rice gene pool. Additionally, *DEP1* is involved in regulating the carbon-nitrogen metabolic balance, which affects grain yield and quality. Overexpression of *DEP1* leads to increased nitrogen uptake and assimilation, although it can also result in an unbalanced carbon-nitrogen metabolism, which may limit further improvements in grain yield and quality.

The research on *DEP1* and its role in rice yield enhancement provides several key insights. Firstly, the *DEP1* gene significantly influences panicle architecture, which is a critical determinant of grain yield. The gain-of-function mutation in *DEP1* enhances grain number per panicle, thereby increasing overall yield. Secondly, the regulation of carbon-nitrogen metabolic balance by *DEP1* suggests that while it can improve nitrogen use efficiency, careful management is required to avoid negative impacts on grain quality. Practical applications of this research include the potential for breeding programs to incorporate the *DEP1* allele to develop high-yielding rice varieties. The findings also highlight the importance of balancing nutrient uptake and assimilation to optimize both yield and quality.

Future research should focus on further elucidating the molecular mechanisms by which *DEP1* regulates panicle architecture and carbon-nitrogen metabolism. Understanding these pathways in greater detail could lead to the development of strategies to mitigate the negative effects of unbalanced carbon-nitrogen metabolism observed in *DEP1*-overexpressed lines. Additionally, exploring the interaction of *DEP1* with other genes involved in panicle development and nutrient metabolism could provide insights into synergistic effects that enhance yield.

From a policy perspective, it is recommended to support the incorporation of *DEP1* alleles into a broader range of rice breeding programs. Policies should also promote research into sustainable agricultural practices to optimize nutrient management, ensuring that the yield-enhancing benefits of *DEP1* are fully realized without compromising grain quality. Additionally, investment in genetic research and biotechnological tools such as CRISPR/Cas9 can accelerate the development of rice varieties with improved yield and stress resistance.

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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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