Rice Genomics and Genetics 2024, Vol.15, No.3, 121-131
http://cropscipublisher.com/index.php/rgg

Feature Review **Open Access**

The Role of *SD1* and *MOC1* in Rice Plant Architecture and Yield Enhancement

Hongli Ma
College of Life Sciences, Fujian Agriculture and Forestry University, Fuzhou, 350002, Fujian, China
Corresponding email: mahongli@fafu.edu.cn

Rice Genomics and Genetics, 2024, Vol.15, No.3 doi: 10.5376/rgg.2024.15.0013
Received: 14 Apr., 2024
Accepted: 15 May, 2024
Published: 25 May, 2024

Preferred citation for this article:
Ma H.L., 2024, The role of *SD1* and *MOC1* in rice plant architecture and yield enhancement, Rice Genomics and Genetics, 15(3): 121-131 (doi: 10.5376/rgg.2024.15.0013)

Abstract Rice plant architecture significantly influences crop yield and resilience, making it a critical focus in agricultural research. This study aims to elucidate the roles of the *SD1* and *MOC1* genes in shaping rice plant structure and enhancing yield. The *SD1* gene, essential for gibberellin biosynthesis, is analyzed for its contributions to dwarfism, stem strength, and overall yield improvements, including lodging resistance and grain filling. Concurrently, the *MOC1* gene, which regulates tillering and branching, is examined for its impact on tillering numbers, root and shoot architecture, and yield optimization. The interplay between *SD1* and *MOC1* is explored, highlighting their synergistic effects on plant growth, balanced morphology, and combined yield contributions. Breeding strategies employing traditional and modern genetic techniques are discussed, with case studies demonstrating the successful integration of these genes into high-yielding and stress-resilient cultivars. Future research directions, including emerging studies on *SD1* and *MOC1*, potential yield enhancements, and sustainability challenges, are considered. The study concludes by summarizing key findings and discussing their implications for future research and breeding programs.

Keywords Rice plant architecture; *SD1* gene; *MOC1* gene; Yield enhancement; Breeding strategies

1 Introduction

Rice (*Oryza sativa*) is a staple food crop that sustains over half of the world's population. The architecture of rice plants, encompassing traits such as plant height, tillering capacity, and stem strength, plays a pivotal role in determining overall crop yield and resilience. Optimal plant architecture not only enhances photosynthetic efficiency and nutrient utilization but also improves resistance to lodging and environmental stresses. As such, understanding the genetic underpinnings of rice plant architecture is crucial for developing high-yielding, resilient rice varieties that can meet the demands of a growing global population and changing climate conditions.

The objective of this study is to systematically examine the roles of two key genes, *SD1* (Semi-Dwarf1) and *MOC1* (*MONOCULM1*), in shaping rice plant architecture and enhancing yield. By exploring the genetic and molecular bases of these genes, their impacts on plant structure, and their contributions to yield improvement, this study aims to provide a comprehensive understanding of their significance and potential applications in rice breeding programs. Furthermore, the study will delve into the interaction between *SD1* and *MOC1*, highlighting their synergistic effects and the integrated benefits they offer to rice cultivation.

SD1 and *MOC1* are central to rice plant architecture and productivity. The *SD1* gene is a well-studied regulator of gibberellin biosynthesis, influencing plant height and stem strength. Variations in *SD1* have been associated with the development of dwarf and semi-dwarf rice varieties, which exhibit enhanced lodging resistance and yield. On the other hand, *MOC1* is crucial for the regulation of tillering and branching, affecting the number of tillers and overall plant morphology. Together, these genes offer a strategic pathway for optimizing plant architecture to achieve higher yield and improved agronomic performance. This study will provide an in-depth analysis of the genetic mechanisms and practical implications of *SD1* and *MOC1* in rice, offering insights into future research and breeding strategies.

2 The *SD1* Gene and Its Role in Rice

2.1 Genetic and molecular basis of *SD1*

The *SD1* gene, known as the "green revolution gene", encodes the enzyme gibberellin 20-oxidase-2 (GA20ox-2), which is crucial in the biosynthesis of gibberellins (GAs), a class of plant growth hormones. The gene consists of three exons and two introns, with mutations in this gene leading to a semi-dwarf phenotype due to reduced GA levels (Ashikari et al., 2002; Monna et al., 2002; Peng et al., 2021). The most common mutations include deletions and single nucleotide substitutions that result in a nonfunctional enzyme, thereby reducing the plant's height (Monna et al., 2002; Spielmeyer et al., 2002).

The *SD1* gene plays a pivotal role in the final steps of GA biosynthesis. Mutations in *SD1* lead to a decrease in bioactive GA levels, which in turn affects plant height and other growth parameters. The gene's expression is regulated by feedback mechanisms involving GA levels, ensuring that GA biosynthesis is tightly controlled (Ashikari et al., 2002; Sasaki et al., 2002). Additionally, interactions with other hormones such as brassinosteroids (BR) further modulate the effects of *SD1* on plant growth (San et al., 2020).

2.2 Impact on plant architecture

The introduction of *SD1* alleles has been instrumental in creating semi-dwarf rice varieties, which are shorter and more robust compared to their wild-type counterparts. This semi-dwarfism is primarily due to the reduced levels of bioactive GAs resulting from the loss-of-function mutations in the *SD1* gene (Figure 1) (Asano et al., 2007; Jia et al., 2020; Peng et al., 2021). These semi-dwarf varieties have been widely adopted in rice breeding programs to improve yield and plant stability (Sasaki et al., 2002; Asano et al., 2007).

The *SD1* gene significantly influences stem length and strength. Semi-dwarf varieties with *SD1* mutations exhibit shorter and sturdier stems, which are less prone to lodging (falling over) under high nitrogen fertilization and heavy grain loads (Ashikari et al., 2002; Spielmeyer et al., 2002; San et al., 2020). This enhanced stem strength is a direct consequence of the reduced GA levels, which limit excessive stem elongation and promote a more compact plant structure (Monna et al., 2002; Peng et al., 2021).

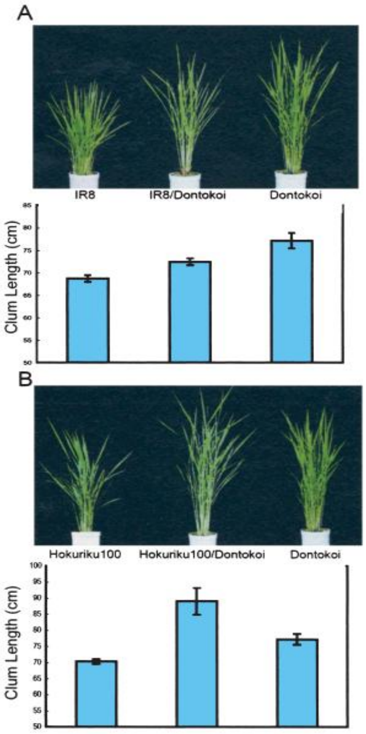


Figure 1 Allelism test of plant heights between Dontokoi and either IR8 (A) or Hokuriku100 (B) (Adopted from Asano et al., 2007)
Image caption: F1 plants from crosses between the parental plants on the left and right are shown in the center (Adopted from Asano et al., 2007)

2.3 Contributions to yield enhancement

One of the most significant contributions of the *SD1* gene to rice yield enhancement is its role in improving lodging resistance. The shorter, sturdier stems of *SD1* mutants are less likely to lodge, even under adverse weather conditions or high nitrogen fertilization, thereby ensuring higher and more stable yields (Sasaki et al., 2002; Asano et al., 2007; San et al., 2020). This trait was a key factor in the success of the "green revolution" rice varieties, such as IR8, which dramatically increased rice production in the 1960s (Ashikari et al., 2002; Peng et al., 2021).

The *SD1* gene also contributes to yield enhancement by improving grain filling and the harvest index. The semi-dwarf varieties tend to allocate more resources to grain production rather than vegetative growth, resulting in a higher harvest index (the ratio of grain yield to total biomass) (Asano et al., 2007; Jia et al., 2020). Additionally, the improved light penetration into the canopy due to the more erect leaf inclination angle in *SD1* mutants further enhances photosynthetic efficiency and grain filling (San et al., 2020). The *SD1* gene plays a crucial role in rice plant architecture and yield enhancement by regulating gibberellin biosynthesis, influencing plant height and stem strength, and improving lodging resistance and grain filling. The widespread adoption of *SD1* mutants has been a cornerstone of modern rice breeding, contributing significantly to global food security.

3 The *MOC1* Gene and Its Role in Rice

3.1 Genetic and molecular basis of *MOC1*

The *MONOCULM1* (*MOC1*) gene plays a critical role in the regulation of rice tillering and overall plant architecture. Located on chromosome 6, *MOC1* encodes a transcription factor that belongs to the GRAS protein family. This gene is essential for the initiation and development of tillers, which are the lateral branches that emerge from the base of the rice plant. Mutations or disruptions in *MOC1* result in the monoculm phenotype, characterized by a single main culm with no tillers, demonstrating the gene's pivotal role in tiller formation and plant morphology (Yu et al., 2020).

The *MOC1* gene functions as a master regulator of tillering and branching in rice. It is expressed in the axillary meristems, where it activates the transcription of downstream genes involved in the initiation and outgrowth of tillers. *MOC1* interacts with various hormonal pathways, including those of auxin and cytokinin, to modulate the balance between tiller bud dormancy and activation. This regulation ensures optimal tillering, contributing to the plant's ability to maximize light capture and nutrient use efficiency.

3.2 Impact on plant architecture

The *MOC1* gene directly influences the number of tillers a rice plant produces. By regulating the activation and growth of axillary buds, *MOC1* determines the extent of tillering, which is a crucial component of rice plant architecture. Increased tillering, controlled by *MOC1*, leads to a bushier plant with more shoots, which can enhance photosynthetic capacity and potential grain production.

Beyond tillering, *MOC1* also impacts the overall root and shoot architecture of rice plants (Figure 2) (Shao et al., 2019). The gene's regulatory functions extend to the coordination of root growth patterns, ensuring a robust root system that can support the increased shoot biomass resulting from enhanced tillering. This integrated development of roots and shoots under the influence of *MOC1* is vital for maintaining plant stability and nutrient uptake, which are essential for high yield performance.

3.3 Contributions to yield enhancement

One of the primary contributions of the *MOC1* gene to rice yield enhancement is through the increase in tiller and panicle numbers. More tillers typically result in more panicles, each of which can produce grains. The effective management of tillering via *MOC1* ensures that these additional panicles are well-developed and capable of supporting a high grain load, thereby directly contributing to increased grain yield per plant (Deng et al., 2022).

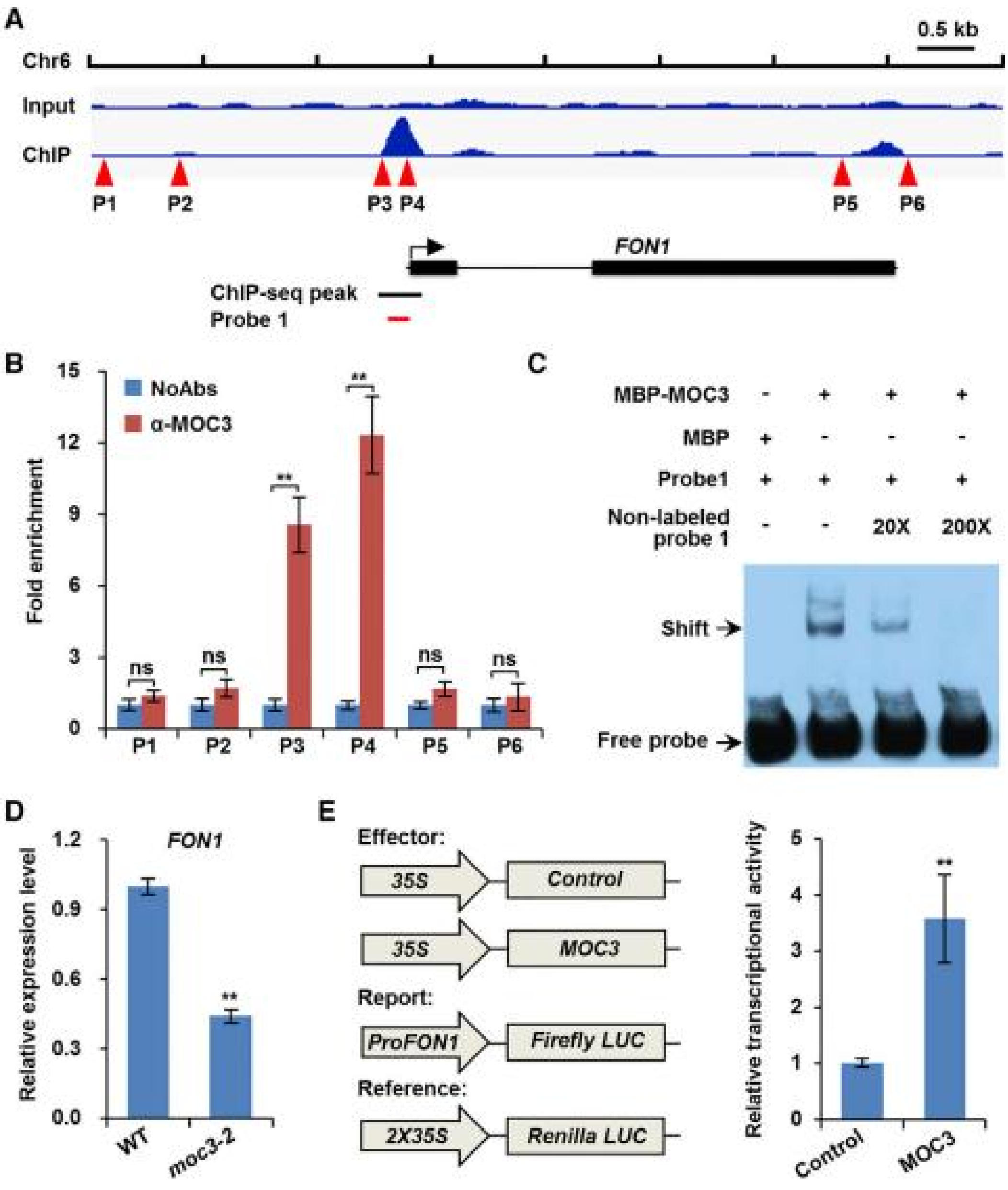


Figure 2 Binding of *MOC3* to *FON1* promoter activates *FON1* expression (Adopted from Shao et al., 2019)

Image caption: (A) MOC3 binding profile on the FON1 promoter; The black line represents the ChIP-seq peak, and the red line indicates probe 1 used in the EMSA experiment; Sites P1 to P6 were used for the ChIP-qPCR experiment; (B) ChIP-qPCR analysis validating *MOC3* binding sites on the *FON1* promoter using *MOC3* polyclonal antibodies in the 0.3 cm shoot bases of wild-type Nipponbare seedlings; Fold enrichment values were normalized against the Ubiquitin promoter; Values are means±SEM (n=3); ***P*<0.01; ns, not significant; (C) EMSA experiment showing that *MOC3* can directly bind to probe 1; Competition was performed with 20-fold and 200-fold excess unlabeled probes; (D) *FON1* expression levels in wild type (WT) and moc3-2; Values are means±SEM (n=3); ***P*<0.01; Ten-day-old seedlings were used for qRT-PCR; (E) Transient transcriptional activity assay showing that MOC3 activates the expression of *FON1* in rice protoplasts; The left panel shows the constructs used in the transient expression assays; Values are means±SD (n=3); ***P*<0.01 (Adapted from Shao et al., 2019)

MOC1 also plays a significant role in optimizing resource allocation within the rice plant. By balancing the growth of tillers and the development of the root system, *MOC1* ensures that the plant can efficiently utilize available resources, such as water and nutrients. This optimization is crucial for sustaining high yields, especially under varying environmental conditions. Efficient resource allocation driven by *MOC1* helps maintain a stable yield and improves the plant's overall fitness and resilience.

The *MOC1* gene is a fundamental regulator of rice plant architecture and yield. Its influence on tillering, root and shoot development, and resource allocation highlights its importance in rice breeding programs aimed at enhancing productivity and resilience. Understanding the genetic and molecular mechanisms of *MOC1* offers valuable insights into the development of high-yielding rice varieties that can meet future food security challenges.

4 Interaction Between *SD1* and *MOC1*

4.1 Genetic interactions and pathways

The interaction between the *SD1* (Semi-Dwarf1) and *MOC1* (*MONOCULM1*) genes plays a crucial role in regulating rice plant growth and development (Zhang et al., 2020). *SD1*, a key gene involved in gibberellin biosynthesis, primarily influences plant height by controlling stem elongation. In contrast, *MOC1* regulates tillering and branching, determining the number of tillers and overall plant morphology. When these two genes interact, they create a synergistic effect that enhances overall plant growth. The dwarfism induced by *SD1* contributes to stronger stems and reduced lodging risk, while the increased tillering driven by *MOC1* leads to a bushier plant structure with more potential sites for grain production. Together, these effects improve plant stability and resource allocation, resulting in robust growth.

SD1 and *MOC1* are part of complex regulatory networks that involve various hormonal pathways, including gibberellins, auxins, and cytokinins (Bhuvaneswari et al., 2020). These hormones interact to balance stem elongation and tiller formation. *SD1* regulates gibberellin levels, which influence not only plant height but also the activation of tiller buds modulated by *MOC1*. This interplay ensures that the rice plant maintains an optimal architecture for maximizing yield. Understanding these regulatory networks is essential for manipulating these genes in breeding programs to achieve desired plant traits.

4.2 Combined impact on plant architecture

The combined action of *SD1* and *MOC1* genes results in a balanced rice plant architecture that maximizes yield potential. *SD1*’s role in reducing plant height and enhancing stem strength complements *MOC1*’s ability to increase tillering. This balance is critical; while increased tillering can enhance grain production, it also requires sturdy stems to support the additional biomass and prevent lodging. The interaction between these genes ensures that the plant can sustain increased tiller numbers without compromising structural integrity (Jia et al., 2020).

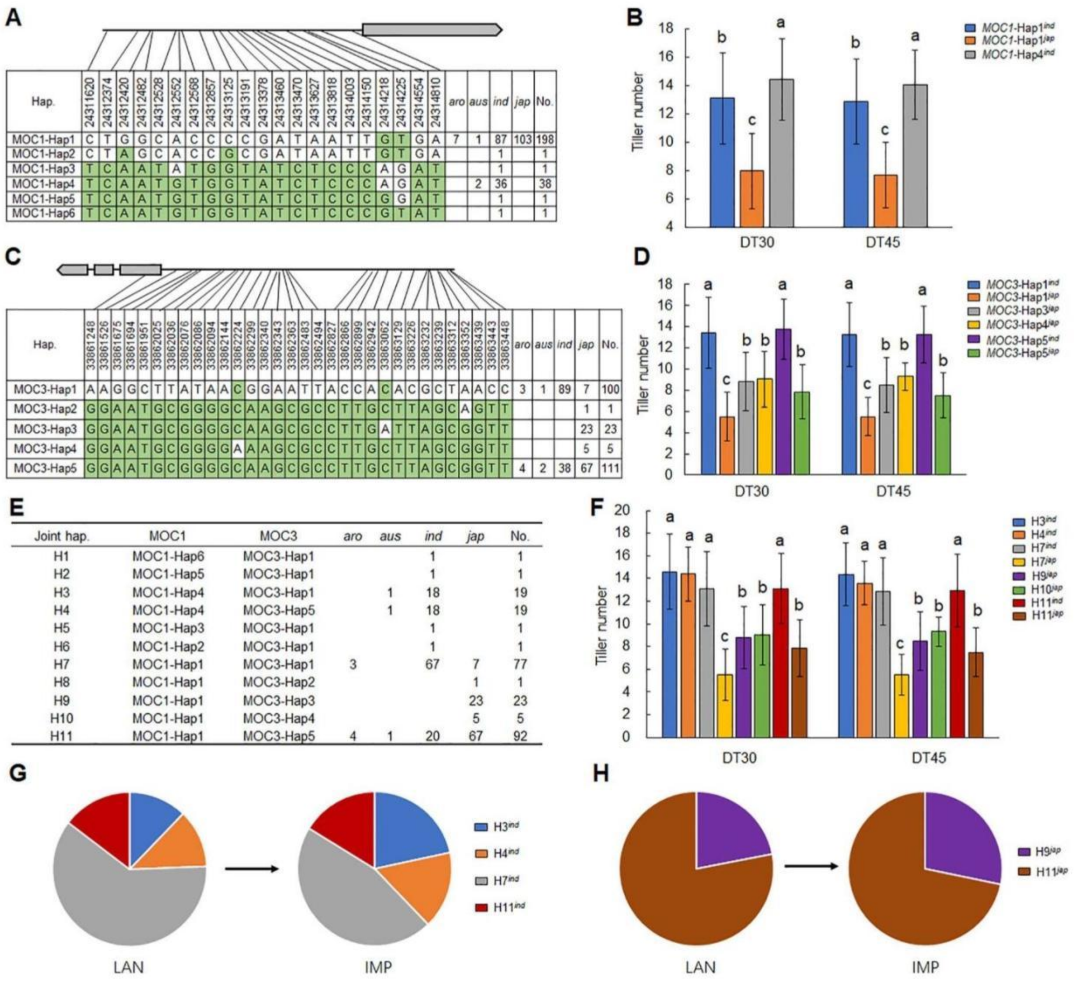
SD1 and *MOC1* together contribute to an integrated plant morphology that optimizes light capture, nutrient use, and overall plant fitness. The semi-dwarf stature conferred by *SD1* allows for more efficient light penetration to lower leaves, while the increased tillering promoted by *MOC1* ensures a fuller canopy that can maximize photosynthetic capacity. This integration of traits leads to a more efficient use of resources and enhances the plant’s ability to thrive in diverse environments.

4.3 Combined contributions to yield

The synergistic effects of *SD1* and *MOC1* on plant architecture directly contribute to maximizing grain production. *SD1* improves stem strength and reduces lodging, ensuring that the plant can support a higher grain load. Meanwhile, *MOC1* increases the number of tillers and panicles, leading to more sites for grain development. This combination enhances the overall grain yield per plant, making these genes valuable targets in rice breeding programs aimed at improving productivity.

Beyond grain production, the interaction between *SD1* and *MOC1* enhances overall plant fitness (Figure 3) (Zhang et al., 2021). The optimized plant architecture resulting from these genes improves resource allocation, water use efficiency, and nutrient uptake. This holistic improvement in plant performance ensures that rice varieties can maintain high yields under a range of environmental conditions, including stress factors such as drought or nutrient deficiency. By enhancing overall plant fitness, *SD1* and *MOC1* contribute to the development of resilient rice varieties that can adapt to changing agricultural landscapes and climate conditions.

The interaction between *SD1* and *MOC1* genes plays a vital role in shaping rice plant architecture and enhancing yield. Their synergistic effects on plant growth, regulatory networks, and combined impact on plant morphology and yield underscore their importance in rice breeding strategies. Understanding and leveraging these interactions can lead to the development of high-yielding, resilient rice varieties that are crucial for global food security.



Hap.	24311620	24312374	24312420	24312482	24312528	24312552	24312568	24312857	24313125	24313191	24313378	24313460	24313470	24313627	24313818	24314003	24314150	24314218	24314225	24314554	24314810	*aro*	*aus*	*ind*	*jap*	No.
MOC1-Hap1	C	T	G	G	C	A	C	C	C	C	G	A	T	A	A	T	T	G	T	G	A	7	1	87	103	198
MOC1-Hap2	C	T	A	G	C	A	C	C	G	C	G	A	T	A	A	T	T	G	T	G	A			1		1
MOC1-Hap3	T	C	A	A	T	A	T	G	G	T	A	T	C	T	C	C	C	A	G	A	T			1		1
MOC1-Hap4	T	C	A	A	T	G	T	G	G	T	A	T	C	T	C	C	C	A	G	A	T		2	36		38
MOC1-Hap5	T	C	A	A	T	G	T	G	G	T	A	T	C	T	C	C	C	G	G	A	T			1		1
MOC1-Hap6	T	C	A	A	T	G	T	G	G	T	A	T	C	T	C	C	C	G	T	A	T			1		1

Hap.	33861248	33861526	33861675	33861694	33861951	33862025	33862036	33862076	33862086	33862094	33862144	33862224	33862299	33862340	33862343	33862363	33862483	33862494	33862827	33862866	33862899	33862942	33863062	33863129	33863226	33863232	33863239	33863312	33863352	33863439	33863443	33863448	*aro*	*aus*	*ind*	*jap*	No.
MOC3-Hap1	A	A	G	G	C	T	T	A	T	A	A	C	G	G	A	A	T	T	A	C	C	A	C	A	C	G	C	T	A	A	C	C	3	1	89	7	100
MOC3-Hap2	G	G	A	A	T	G	C	G	G	G	G	C	A	A	G	C	G	C	C	T	T	G	C	T	T	A	G	C	A	G	T	T				1	1
MOC3-Hap3	G	G	A	A	T	G	C	G	G	G	G	C	A	A	G	C	G	C	C	T	T	G	A	T	T	A	G	C	G	G	T	T				23	23
MOC3-Hap4	G	G	A	A	T	G	C	G	G	G	G	A	A	A	G	C	G	C	C	T	T	G	C	T	T	A	G	C	G	G	T	T				5	5
MOC3-Hap5	G	G	A	A	T	G	C	G	G	G	G	C	A	A	G	C	G	C	C	T	T	G	C	T	T	A	G	C	G	G	T	T	4	2	38	67	111

Joint hap.	MOC1	MOC3	*aro*	*aus*	*ind*	*jap*	No.
H1	MOC1-Hap6	MOC3-Hap1			1		1
H2	MOC1-Hap5	MOC3-Hap1			1		1
H3	MOC1-Hap4	MOC3-Hap1		1	18		19
H4	MOC1-Hap4	MOC3-Hap5		1	18		19
H5	MOC1-Hap3	MOC3-Hap1			1		1
H6	MOC1-Hap2	MOC3-Hap1			1		1
H7	MOC1-Hap1	MOC3-Hap1	3		67	7	77
H8	MOC1-Hap1	MOC3-Hap2				1	1
H9	MOC1-Hap1	MOC3-Hap3				23	23
H10	MOC1-Hap1	MOC3-Hap4				5	5
H11	MOC1-Hap1	MOC3-Hap5	4	1	20	67	92

Figure 3 Haplotype analysis of *GNP6*/*MOC1* and *MOC3* (Adopted from Zhang et al., 2021)

Image caption: A: Haplotype frequencies of GNP6/MOC1; B: Tiller numbers in GNP6/MOC1 30 and 45 days post anthesis; Data are means±s.d., n=87, 103, and 36 for *MOC1*-Hap1ind, *MOC1*-Hap1jap and MOC1-Hap4ind, respectively; C: Haplotype frequencies for *MOC3*; D: Tiller numbers of *MOC3* haplotypes; Data are means±s.d., n=89, 7, 23, 5, 38 and 67 for MOC3-Hap1ind, MOC3-Hap1jap, MOC3-Hap3jap, MOC3-Hap4jap, MOC3-Hap5ind, and MOC3-Hap5jap, respectively; E: Joint haplotypes of *GNP6*/*MOC1* and *MOC3*; F: Tiller numbers of different joint haplotypes; Data are means±s; d., n=18, 18, 67, 7, 23, 5, 20 and 67 for H3ind, H4ind, H7ind, H7jap, H9jap, H10jap, H11ind and H11jap, respectively; Different lowercase letters above the error bar indicate significant differences between the means (*P*>0.05, Student's t-test); G-H: Frequencies of joint haplotypes in landrace (LAN) and improved (IMP) accessions within the ind (G) and jap (H) subpopulations (Adopted from Zhang et al., 2021)

5 Breeding Strategies for Enhancing *SD1* and *MOC1*

5.1 Traditional breeding approaches

Traditional breeding approaches for enhancing *SD1* and *MOC1* in rice primarily involve selection and hybridization techniques. Selection involves identifying and choosing plants with desirable traits, such as optimal plant height and improved yield, and using them as parents for the next generation. Hybridization, on the other hand, involves crossing different varieties to combine favorable traits from both parents. For instance, the study by (Zhang et al., 2020) demonstrated the effectiveness of selecting elite *SD1* alleles to achieve ideal plant height and lodging resistance. The research highlighted the importance of allele variation in *SD1*, which was a major factor for plant height segregation in breeding populations from an indica and japonica cross. The study also identified the potential value of the *SD1Jap* allele for hybrid rice breeding, suggesting its compatibility with some recently developed hybrid varieties in China.

Mutation breeding is another traditional approach that involves inducing mutations to create genetic variability, which can then be exploited to develop new varieties with desirable traits. This method can be particularly useful for enhancing traits controlled by single genes, such as *SD1*. The study by (San et al., 2020) explored the role of the *SD1* gene in regulating leaf inclination angle, which is crucial for improving canopy photosynthesis and dry matter production. By manipulating the *SD1* gene, researchers were able to enhance light penetration into the canopy, thereby improving rice yield through better lodging resistance.

5.2 Modern genetic techniques

Marker-assisted selection (MAS) is a modern genetic technique that uses molecular markers to select plants with desirable traits more efficiently. This method allows for the precise identification of specific alleles associated with traits like plant height and yield. The study by (Zhang et al., 2020) utilized newly developed functional markers to characterize different *SD1* alleles, demonstrating high efficiency for genotyping a large set of germplasms. This approach can significantly accelerate the breeding process by enabling the early selection of plants with favorable *SD1* alleles.

CRISPR and other gene-editing technologies offer powerful tools for directly modifying the genetic makeup of plants to enhance traits like those controlled by *SD1* and *MOC1*. These techniques allow for precise edits to be made to the DNA, enabling the creation of new varieties with improved characteristics. Although the provided studies did not specifically mention the use of CRISPR for *SD1* and *MOC1*, the potential for such technologies in rice breeding is immense, given their ability to target and modify specific genes with high precision.

5.3 Integrating *SD1* and *MOC1* in breeding programs

Successful integration of *SD1* and *MOC1* in breeding programs can be illustrated through various case studies. For example, the study by (Zhang et al., 2020) described a breeding practice where the null *SD1* allele was introgressed into the elite japonica variety Daohuaxiang, which suffers from severe lodging. The improved semi-dwarf line demonstrated enhanced agronomic performance, showcasing the practical application of *SD1* alleles in breeding programs. Similarly, the study by (San et al., 2020) highlighted the use of *SD1* mutants to improve leaf inclination angle and canopy photosynthesis, further emphasizing the role of *SD1* in successful breeding strategies.

While there are significant opportunities for enhancing rice plant architecture and yield through the manipulation of *SD1* and *MOC1*, several challenges remain. One major challenge is the complex epistatic interactions between different alleles and genetic backgrounds, as noted in the study by (Zhang et al., 2020). Additionally, the integration of modern genetic techniques like CRISPR requires careful consideration of regulatory and ethical issues. However, the potential benefits, such as improved yield, lodging resistance, and canopy photosynthesis, present substantial opportunities for future research and breeding programs.

Both traditional and modern breeding strategies offer valuable approaches for enhancing *SD1* and *MOC1* in rice. By leveraging techniques like selection, hybridization, marker-assisted selection, and gene editing, researchers can develop new rice varieties with improved plant architecture and yield, addressing the growing demand for food security.

6 Case Studies and Practical Applications

6.1 Successful varieties featuring *SD1* and *MOC1*

The identification and utilization of the *SD1* gene have been pivotal in the development of high-yielding rice varieties. The semi-dwarf phenotype conferred by the *SD1* allele has been instrumental in creating cultivars with increased lodging resistance, allowing for higher nitrogen fertilizer application and subsequently higher yields. Notable examples include Guang-chang-ai and IR8, which were among the first high-yielding varieties to capitalize on the semi-dwarf trait, significantly improving rice yields in China and other regions (Peng et al., 2021). Additionally, the fine-tuning of SPL gene expression has been shown to enhance panicle branching and grain number, further contributing to yield improvements in rice (Wang and Zhang, 2017).

The *MOC1* gene, in conjunction with *MOC3*, plays a crucial role in regulating tiller bud outgrowth, which is essential for optimal plant architecture and yield. The interaction between *MOC1* and *MOC3* upregulates the expression of *FON1*, promoting tiller formation and enhancing overall plant resilience (Figure 4) (Shao et al., 2019). Furthermore, modifications in root system architecture, such as those involving the DRO1 homolog, have been shown to improve rice yields in saline paddy fields by enabling plants to avoid stress conditions, thereby enhancing their resilience and productivity (Kitomi et al., 2020).

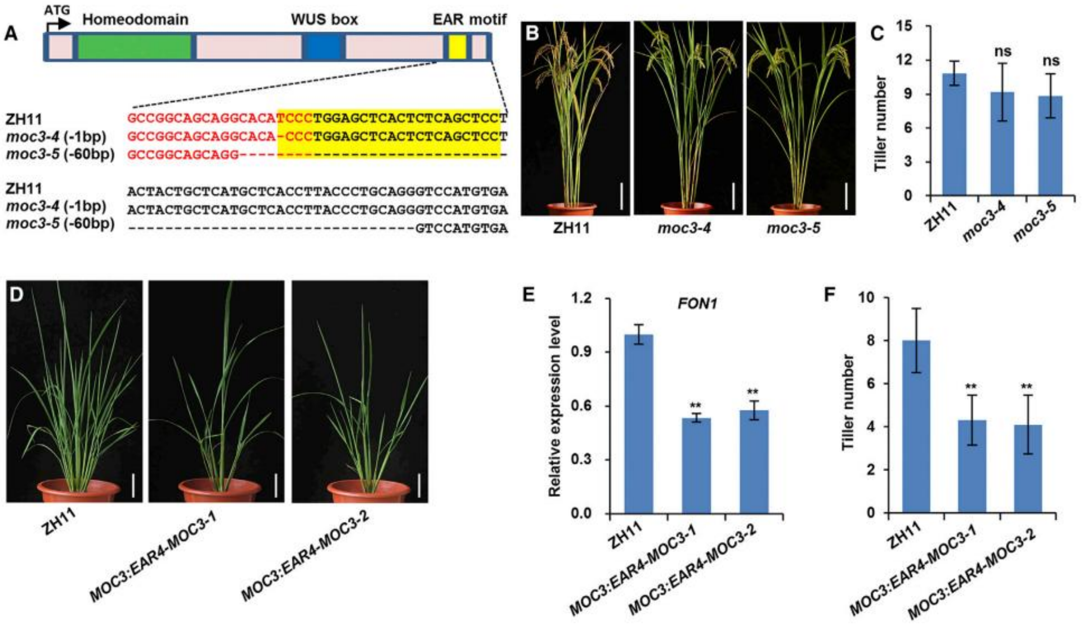


Figure 4 *EAR* motif of *MOC3* is not required for its function in tiller formation regulation (Adopted from Shao et al., 2019)

Image caption: (A) Generation of moc3-4 and moc3-5 by CRISPR/Cas9 technology; Yellow box represents the sequence encoding the EAR motif; Red letters highlight the single guide RNA (sgRNA) target; (B) Gross morphologies of ZH11, moc3-4, and moc3-5; Scale bars, 10 cm; (C) Statistical analysis of tiller numbers of ZH11, moc3-4, and moc3-5; Values are means±SD (n=6); ns indicates no significant difference at $P<0.01$ (two-tailed Student's t-test); (D) Gross morphologies of ZH11, MOC3:EAR4-MOC3-1, and MOC3:EAR4-MOC3-2; Scale bars, 10 cm; (E) Relative expression levels of FON1 in ZH11, MOC3:EAR4-MOC3-1, and MOC3:EAR4-MOC3-2; Values are means±SEM (n=3); $^{**}P<0.01$ (two-tailed Student's t-test); (F) Statistical analysis of tiller number of ZH11, MOC3:EAR4-MOC3-1, and MOC3:EAR4-MOC3-2; Values are means±SD (n=10); $^{**}P<0.01$ (two-tailed Student's t-test) (Adopted from Shao et al., 2019)

6.2 Field performance and agronomic benefits

Field trials have consistently demonstrated the agronomic benefits of varieties featuring the *SD1* and *MOC1* genes. For instance, varieties carrying the *SD1* allele have shown significant improvements in yield due to their semi-dwarf stature, which reduces lodging and allows for higher fertilizer application (Peng et al., 2021). Similarly, the cooperative action of *MOC1* and *MOC3* in promoting tiller bud outgrowth has been linked to increased tiller numbers and improved yield performance in various field conditions (Shao et al., 2019). These genetic modifications have been validated through extensive yield trials, confirming their effectiveness in enhancing rice productivity.

The adoption of high-yielding and stress-resilient rice varieties by farmers has been widespread, driven by the tangible benefits observed in field performance. Farmers have reported increased yields and improved crop resilience, particularly in regions prone to abiotic stresses such as salinity. The success of varieties featuring the *SD1* gene, such as IR8, has been well-documented, with farmers noting the advantages of reduced lodging and higher fertilizer efficiency (Peng et al., 2021). Additionally, the practical applications of *MOC1* and *MOC3* in enhancing tiller formation have garnered positive feedback from farmers, who have observed better plant architecture and higher yields (Shao et al., 2019). The integration of these genetic advancements into breeding programs continues to support sustainable agricultural practices and food security.

7 Future Prospects and Challenges

7.1 Emerging research on *SD1* and *MOC1*

Recent studies have significantly advanced our understanding of the roles of *SD1* and *MOC1* in rice plant architecture and yield enhancement. The restoration of wild-type *SD1* in modern semi-dwarf cultivars has shown promising results, nearly doubling plant height and increasing total grain yield per panicle (Jia et al., 2020). Additionally, the identification and utilization of various *SD1* alleles, such as *SD1*Jap and *SD1*Ind, have demonstrated their potential in breeding programs to optimize plant height and improve yield (Zhang et al., 2020a). The discovery of novel alleles like *GNP6* of *MOC1*, which regulates panicle and tiller development, further enriches the genetic resources available for rice breeders (Zhang et al., 2020b).

7.2 Potential for further yield enhancement

The potential for further yield enhancement lies in the fine-tuning of gene expression and the strategic combination of beneficial alleles. For instance, the manipulation of SPL gene expression has been shown to optimize plant architecture, thereby increasing grain number (Wang and Zhang, 2017). Combining alleles such as sdt and *SD1* has resulted in a significant yield increase, suggesting that pyramiding multiple beneficial alleles could be a viable strategy for future breeding programs (Zhao et al., 2015). Moreover, the weak functional allele *SD1*-EQ from japonica rice has been identified as a valuable genetic resource for improving indica rice lines, indicating the potential for cross-subspecies breeding to enhance yield (Yu et al., 2020).

7.3 Addressing climate change and sustainability

Addressing climate change and sustainability is crucial for the future of rice cultivation. The development of rice varieties with improved lodging resistance and nitrogen utilization, as conferred by the *SD1* allele, is essential for maintaining high yields under varying environmental conditions (Peng et al., 2021). Additionally, understanding the molecular basis of plant architecture and grain quality can lead to the development of elite varieties that are both high-yielding and resilient to climate change. The integration of modern biotechnological tools, such as CRISPR/Cas9, can accelerate the development of climate-resilient rice varieties.

7.4 Policy and regulatory considerations

The successful implementation of advanced breeding techniques and the introduction of new rice varieties require supportive policy and regulatory frameworks. Policymakers must ensure that regulations facilitate the adoption of genetically modified and genome-edited crops while addressing public concerns about food safety and environmental impact. Furthermore, international collaboration and knowledge sharing are essential to maximize the benefits of research advancements in *SD1* and *MOC1* for global food security. Encouraging public and private sector partnerships can also drive innovation and investment in sustainable rice production practices. The emerging research on *SD1* and *MOC1*, combined with advanced breeding strategies and supportive policies, holds great promise for enhancing rice yield and sustainability in the face of global challenges.

8 Concluding Remarks

The role of the *SD1* and *MOC1* genes in rice plant architecture and yield enhancement has been extensively studied, revealing significant insights into their functions and applications. The *SD1* gene, encoding the GA20ox oxidase involved in gibberellin biosynthesis, has been pivotal in the development of semi-dwarf rice varieties that contributed to the Green Revolution. Restoration of the wild-type *SD1* gene in modern semi-dwarf cultivars has been shown to nearly double plant height, increase total grain yield per panicle, and elongate the second-leaf length. This restoration also affects gene expression profiles, particularly in the gibberellin pathway and related metabolic networks, defense responses, and catabolic processes. The identification and utilization of *SD1* mutants have significantly improved rice yields by conferring lodging resistance and enabling high nitrogen fertilizer use.

Future research should focus on further elucidating the molecular mechanisms by which *SD1* and *MOC1* influence plant architecture and yield. This includes exploring the pleiotropic effects of these genes and their interactions with other metabolic and defense pathways. Additionally, the identification of new alleles of *SD1* through mutagenesis and genome editing holds promise for enhancing the genetic diversity and resource base for semi-dwarf breeding programs. Investigating the balance between gibberellin and jasmonic acid pathways in relation to *SD1* could provide deeper insights into optimizing growth and defense responses in rice.

The advancements in understanding the roles of *SD1* and *MOC1* in rice have not only contributed to historical yield improvements but also offer pathways for future innovations in rice breeding. By leveraging genetic insights and modern biotechnological tools, it is possible to develop new rice varieties that combine high yield, robust growth, and resilience to environmental stresses. Continued research in this area will be crucial for meeting the global food demand and ensuring sustainable agricultural practices.

Funding

Science and Technology Project of State Administration of Science, Technology and Industry for National Defense, Seed Innovation and Industrialization Project of Fujian Province (zycxny2021003) Science and Technology Innovation Special Fund Project of Fujian Agriculture and Forestry University (KFB23198).

Acknowledgments

The CropSci Publisher appreciates the feedback from two anonymous peer reviewers on the manuscript of this study, whose careful evaluation and constructive suggestions have contributed to the improvement of the manuscript.

Conflict of Interest Disclosure

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

References

Asano K., Takashi T., Miura K., Qian Q., Kitano H., Matsuoka M., and Ashikari M., 2007, Genetic and molecular analysis of utility of *SD1* alleles in rice breeding, Breeding Science, 57(1): 53-58.
https://doi.org/10.1270/JSBBS.57.53

Ashikari M., Sasaki A., Ueguchi-Tanaka M., Itoh H., Nishimura A., Datta S., Ishiyama K., Saito T., Kobayashi M., Khush G., Kitano H., and Matsuoka M., 2002, Loss-of-function of a rice gibberellin biosynthetic gene, GA20 oxidase (GA20ox-2), led to the rice ‘Green Revolution’, Breeding Science, 52(2): 143-150.
https://doi.org/10.1270/JSBBS.52.143

Bhuvaneswari S., Krishnan S., Ellur R., Vinod K., Bollinedi H., Bhowmick P., Bansal V., Nagarajan M., and Singh A., 2020, Discovery of a novel induced polymorphism in *SD1* gene governing semi-dwarfism in rice and development of a functional marker for marker-assisted selection, Plants, 9(9): 1198.
https://doi.org/10.3390/plants9091198

Deng X., Wang J., Liu X., Yang J., Zhou M., Kong W., Jiang Y., Ke S., Sun T., and Li Y., 2022, QTL Analysis and heterosis loci of effective tiller using three genetic populations derived from Indica-Japonica crosses in rice, Agronomy, 12(9): 2171.
https://doi.org/10.3390/agronomy12092171

Jia X., Yu L., Tang M., Tian D., Yang S., Zhang X., and Traw M., 2020, Pleiotropic changes revealed by in situ recovery of the semi-dwarf gene *SD1* in rice, Journal of Plant Physiology, 248: 153141.
https://doi.org/10.1016/j.jplph.2020.153141

Kitomi Y., Hanzawa E., Kuya N., Inoue H., Hara N., Kawai S., Kanno N., Endo M., Sugimoto K., Yamazaki T., Sakamoto S., Sentoku N., Wu J., Kanno H., Mitsuda N., Toriyama K., Sato T., and Uga Y., 2020, Root angle modifications by the DRO1 homolog improve rice yields in saline paddy fields, Proceedings of the National Academy of Sciences of the United States of America, 117(35): 21242-21250.
https://doi.org/10.1073/pnas.2005911117

Monna L., Kitazawa N., Yoshino R., Suzuki J., Masuda H., Maehara Y., Tanji M., Sato M., Nasu S., and Minobe Y., 2002, Positional cloning of rice semidwarfing gene, sd-1: rice "green revolution gene" encodes a mutant enzyme involved in gibberellin synthesis, DNA Research, 9(1): 11-7.
https://doi.org/10.1093/DNARES/9.1.11

Peng Y., Hu Y., Qian Q., and Ren D., 2021, Progress and prospect of breeding utilization of green revolution gene *SD1* in rice, Agriculture, 11(7): 611.
https://doi.org/10.3390/agriculture11070611

San N., Suzuki K., Soda K., Adachi S., Kasahara H., Yamamoto T., Ikka T., Kondo K., Yamanouchi U., Sugimoto K., Nagamura Y., Hirasawa T., and Ookawa T., 2020, Semi-dwarf 1 (*SD1*) gene enhances light penetration into the canopy through regulating leaf inclination angle in rice, Field Crops Research, 246: 107694.
https://doi.org/10.1016/j.fcr.2019.107694

San N., Suzuki K., Soda K., Adachi S., Kasahara H., Yamamoto T., Ikka T., Kondo K., Yamanouchi U., Sugimoto K., Nagamura Y., Hirasawa T., and Ookawa T., 2020, *Semi-dwarf 1* (*SD1*) gene enhances light penetration into the canopy through regulating leaf inclination angle in rice, Field Crops Research, 246: 107694.

https://doi.org/10.1016/j.fcr.2019.107694

Sasaki A., Ashikari M., Ueguchi-Tanaka M., Itoh H., Nishimura A., Swapan D., Ishiyama K., Saito T., Kobayashi M., Khush G., Kitano H., and Matsuoka M., 2002, Green revolution: a mutant gibberellin-synthesis gene in rice, Nature, 416: 701-702.
https://doi.org/10.1038/416701a

Shao G., Lu Z., Xiong J., Wang B., Jing Y., Meng X., Liu G., Ma H., Liang Y., Chen F., Wang Y., Li J., and Yu H., 2019, Tiller bud formation regulators *MOC1* and MOC3 cooperatively promote tiller bud outgrowth by activating FON1 expression in rice, Molecular Plant, 12(8): 1090-1102.
https://doi.org/10.1016/j.molp.2019.04.008

Spielmeyer W., Ellis M., and Chandler P., 2002, Semidwarf (sd-1), “green revolution” rice, contains a defective gibberellin 20-oxidase gene, Proceedings of the National Academy of Sciences of the United States of America, 99(13): 9043-9048.
https://doi.org/10.1073/pnas.132266399

Wang L., and Zhang Q., 2017, Boosting rice yield by fine-tuning SPL gene expression, Trends in Plant Science, 22(8): 643-646.
https://doi.org/10.1016/j.tplants.2017.06.004

Wu T., Ali A., Wang J., Song J., Fang Y., Zhou T., Luo Y., Zhang H., Chen X., Liao Y., Liu Y., Xu P., and Wu X., 2021, A homologous gene of OsREL2/ASP1, ASP-LSL regulates pleiotropic phenotype including long sterile lemma in rice, BMC Plant Biology, 21(1): 390.
https://doi.org/10.1186/s12870-021-03163-7

Yu Y., Hu X., Zhu Y., and Mao D., 2020, Re-evaluation of the rice ‘Green Revolution’ gene: the weak allele *SD1*-EQ from japonica rice may be beneficial for super indica rice breeding in the post-green revolution era, Molecular Breeding, 40: 1-12.
https://doi.org/10.1007/s11032-020-01164-2

Zhang L., Bian Z., Ma B., Li X., Zou Y., Xie D., Liu J., Ren Y., Zhang C., Wang J., Ye S., Deng Y., Li Q., Zhang X., He Z., and Liu Q., 2020, Exploration and selection of elite *SD1* alleles for rice design breeding, Molecular Breeding, 40: 1-16.
https://doi.org/10.1007/s11032-020-01161-5

Zhang M., Wang Y., Chen X., Xu F., Ding M., Ye W., Kawai Y., Toda Y., Hayashi Y., Suzuki T., Zeng H., Xiao L., Xiao X., Xu J., Guo S., Yan F., Shen Q., Xu G., Kinoshita T., and Zhu Y., 2021, Plasma membrane H+-ATPase overexpression increases rice yield via simultaneous enhancement of nutrient uptake and photosynthesis, Nature Communications, 12(1): 735.
https://doi.org/10.1038/s41467-021-20964-4

Zhang Z., Sun X., Ma X., Xu B., Zhao Y., Ma Z., Li G., Khan N., Pan Y., Liang Y., Zhang H., Li J., and Li Z., 2020, GNP6, a novel allele of *MOC1*, regulates panicle and tiller development in rice, Crop Journal, 9(1): 57-67.
https://doi.org/10.1016/j.cj.2020.04.011

Zhao M., Liu B., Wu K., Ye Y., Huang S., Wang S., Wang Y., Han R., Liu Q., Fu X., and Wu Y., 2015, Regulation of OsmiR156h through alternative polyadenylation improves grain yield in rice, PLoS One, 10(5): e0126154.
https://doi.org/10.1371/journal.pone.0126154