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Genetic and Epigenetic Regulatory Mechanism of Rice Panicle Development

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Abstract. Rice panicle architecture is a key agronomical trait that directly contributes to grain productivity. The complexity of the developmental process of the young panicle determines the complexity of its regulatory molecular mechanism. This paper briefly introduces the general process of panicle development and summarizes the important genes/quantitative trait loci regulating panicle development, identified and characterized by mutant screening and map cloning in recent years. According to their roles in the rice panicle development process, these genes are divided into 3 categories: initiation and maintenance of axillary meristems, size of meristem, and elongation of the branches. In recent years, knowledge on the epigenetic regulatory mechanism of panicle development has improved. In addition, development of the young panicle has been confirmed to be closely related to the regulation of plant hormones. Finally, the new genome editing tool clustered regularly interspaced short palindromic repeats/associated protein-9 nuclease and epigenome-wide association studies are expected to contribute to further understand the molecular mechanisms of panicle development, which might help improving panicle traits for increasing grain yield.

23 September 2023 23:24:08

INTRODUCTION

Rice is one of the most important food crops and is the primary nutritive source for more than one-half of the global population. However, given the continuous and rapid growth of the world's population and continuous decrease in arable land, grain yield must be sustainably improved. As such, increasing rice yield while decreasing rice-planting area has always been a major focus of rice breeding plans [1,2]. In the past half-century, there were two major breakthroughs in improving rice yield: semi-dwarf breeding and hybrid breeding. Furthermore, Green Super Rice has been considered "the second green revolution" because of its high yield [3].

Rice yield is a complex agronomic characteristic composed of four typical traits: number of panicles, number of spikelets per panicle, seed setting, and grain weight. Accordingly, rice panicle architecture is one of the most important agronomical traits that directly contributes to rice production [4]. However, rice is a model monocot species, and thus the structure and developmental regulation of rice inflorescence are very distinct from those of other dicot species. Thus, studies of panicle architecture are not only important for improving rice varieties and creating new germplasm resources, but also have important theoretical significance for improving regulation models of monocot inflorescences.

This review briefly summarizes the recent advances in elucidating the genetic and epigenetic regulatory mechanisms underlying rice panicle architecture, and discusses the significance of these results in rice genetic improvement and future development trends.

DEVELOPMENT OF THE YOUNG PANICLE

The complexity of adult plant architecture is generated by lateral growth, which is determined by the activity of post-embryonically produced secondary meristems, known as axillary meristems (AMs). In rice (*Oryza sativa*), an AM produced at the axil of the leaf generates a new shoot branch known as the tiller, whereas an AM produced in the

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inflorescence generates a higher-order inflorescence branch—the rachis branch—which bears a grass-specific structural unit of the inflorescence, the spikelet.

The growth cycle of higher plants is divided into the vegetative and reproductive phases. During the vegetative phase, the shoot apical meristem (SAM) produces the leaf primordium (LP), which is a small bulge formed on the gradually inflated SAM. After photoperiod induction, rice transitions from the vegetative to the reproductive phase, and the primary SAM produces several AMs that become panicle branches. First, the SAM converts into an inflorescence meristem (IM), which is the initial stage of panicle development in rice. Second, the IM generates primary branch meristems (PBMs) and supplies cells to form the rachis. When PBMs are differentiated, reach a certain number, and elongate to a certain extent, secondary branch meristems (SBMs) emerge from the basal regions. Third, the PBMs and SBMs convert to terminal spikelet meristems (TSMs) at the top of the branch and lateral spikelet meristems (LSMs) on the lateral branch. Finally, spikelet meristems are converted into floret meristems, which produce floral organs. The course of panicle development and a sketch of the mature rice panicle are shown in Figure 1.

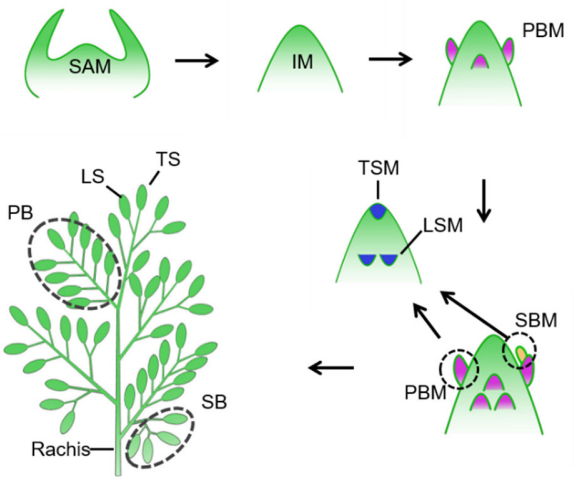

FIGURE 1. The course of the panicle development and the sketch of mature rice inflorescence. SAM, shoot apical meristem; IM, inflorescence meristem; RM, rachis meristem; PBM, primary branch meristem; SBM, secondary branch meristem; TSM, terminal spikelets meristem; LSM, lateral spikelets meristem; PB, primary branch; SB, secondary branch; LS, lateral spikelets; TS, terminal spikelets

KEY GENES CONTROLLING PANICLE DEVELOPMENT

The formation of panicle branches in rice is more complicated than that of the inflorescence branch of *Arabidopsis thaliana*. Numerous genes involved in the formation of diverse panicle types (erect, bent, dense, sparse, long, and short) have been cloned and functionally characterized by screening mutants and by map-based cloning, using from a single AM to a panicle. Because the size and shape of the panicle is directly related to grain yield, breeders aim to produce rice with large and erect panicles. Current studies suggest that the size of the panicle is determined by the initiation and maintenance of AMs, meristem size, and branch elongation. Based on these three aspects, we briefly explain the functions of the genes involved in regulating panicle differentiation.

In the past decades, numerous genes controlling the establishment of meristem identity have been shown to influence panicle development. *Lax Panicle 1* (*LAX1*), encoding a plant-specific basic helix-loop-helix transcription factor, participates in the initiation and maintenance of AMs and promotes the formation of lateral meristems in the inflorescence. In *lax1* mutants, the number of primary branches (PBs), secondary branches (SBs), and seeds was severely reduced and, in some *LAX1* allelic mutants TSMs grew indefinitely [5-7]. Furthermore, LAX1 can physically interact with Lax Panicle 2 (LAX2) encoding a nuclear protein that contains a plant-specific conserved domain to form a complex that regulates AM formation. The phenotypes of *lax2* and *lax1* mutants are very similar, their PBs and SBs were reduced, and the lateral spikelets (LSs) disappeared. The phenotype of the *lax1lax2* double mutant is more intense, indicating that *LAX1* and *LAX2* play important roles in maintaining the characteristics of rice AMs [8].

23 September 2023 23:24:08

Small panicle (*SPA*) is functionally redundant with *LAX1* and controls the production path of rice AMs. In *spa* mutants, branch and spikelet numbers per panicle decreased, the PB at the panicle base was absent, all first branches were shorter, second branches decreased although forming LSs, and branch number decreased relative to wild type lines. In the double mutant *lax1-1spa*, the panicle was a linear structure lacking all branches [6].

The *Aberrant Panicle Organization 2/Rice LEAFY (LFY) Homolog* (*APO2/RFL*), the orthologous gene of *A. thaliana LFY*, acts on the early development of the inflorescence, and its expression is preceded by that of *LAX1* [9]. Unlike *LFY*, *APO2* determines the identity of the entire inflorescence meristem rather than the specific floral meristem. Furthermore, *APO2* can interact with *Aberrant Panicle Organization 1* (*APO1*), the orthologous gene of *A. thaliana Unusual Floral Organs* (*UFO*), to coordinately regulate panicle development in rice. Mutants *apo1* and *apo2* showed fewer branches and grains per spike than wild-type rice by antedating the transition from the branch primordium to the spikelet primordium [9-11]. As the orthologous gene of maize *Branched Silkless 1* (*BD1*) in rice, *Frizzy Panicle* (*FZP*), the major negative regulator of *RFL*, has become a marker gene for the spikelet meristem in Gramineae, and can up-regulate the formation of the spikelet meristem and down-regulate the formation of the branch meristem [5,12,13].

The plant-specific *Squamosa Promoter Binding Protein Like* (*SPL*) gene family is a target of rice miR156 [14,15]. The *OsSPL14* gene is expressed in the LP, bract LP, mature leaf, and spikelet, but not in the meristem, and OsSPL14 inhibits the over-development of axillary buds. *Panicle Phytomer 2* (*PAP2*)/*OsMADS34,* which is directly regulated by *OsSPL14*, maintains the normal order of spikelet development by restricting the excessive primary branch and preventing PBMs prematurely transforming into secondary branches [16,17]. *Rice Centroradialis 1* (*RCN1*), a homologue of *A. thaliana Terminal Flower 1* (*TFL1*) in rice, is also an important gene regulating the formation of spikelet meristems, and its expression is inhibited by six MADS-box genes including *OsMADS34*. Overexpression of *RCN1* and *Rice Centroradialis 2* (*RCN2*) can prolong the transition from vegetative to reproductive growth; plants are characterized by a delay in the transformation of the branch meristem into the floret structure, resulting in a significant increase in the number of branches and in dense panicles [18].

Aberrant Spikelet and Panicle 1 (*ASP1*), a recently cloned *A. thaliana Topless/Topless Related* (*TPL/TPR*) gene, and *Ramosa Enhancer Locus 2* (*REL2*), the homolog of maize *RAMOSA* in rice, encode a transcription factor that influences IM, BM, and SM formation and maintains the decisive ability of a variety of cells in the meristems [19]. *Tongari Boushi* (*TOB*) genes, which are expressed in organ primordia, are likely to act in a non-cell autonomous manner on the meristems, and regulate the maintenance and identity of spikelet meristems and branch meristems [20]. Many of these genes can interact with each other or be regulated by each other in order to control biological processes.

In addition to the genes described above that regulate the establishment of meristem identity, several genes controlling meristem activity to determine meristem size are also vital for panicle architecture. Cytokinin (CK) promotes cell division and plays a conserved and significant role in regulating the size and activity of reproductive meristems, thereby affecting branching in dicots [21,22]. Lowering CK concentration or blocking CK signaling leads to reduced SAM meristem activity [23-25]. *Lonely Guy* (*LOG*) encodes a CK-activating enzyme with specific DNA hydrolase activity, directly altering non-active CK and its nucleotide complex to a free form in order to perform its biological function. Loss of *LOG* function leads to premature termination of SAM development, indicating that CK is essential for maintaining meristem activity [26]. *Grain Number 1a*/*Cytokinin Oxidase 2* (*Gn1a/OsCKX2*), encoding a CK oxidase-degrading CK, is a major quantitative trait locus (QTL) that controls grain number per panicle. Reduced expression of rice *Gn1a*/*OsCKX2* resulted in CK accumulation in the IM, increasing spikelet number and grain number per panicle, ultimately increasing rice yield [27]. Several genes have been reported to regulate CK levels in the reproductive meristem by regulating the transcription levels of *OsCKX2*. The expression of *OsCKX2* can be directly up-regulated by *Drought and Salt Tolerance* (*DST*), a rice zinc-finger transcription factor. A semi-dominant allele of *DST* can increase CK levels by reducing the expression of *OsCKX2*, thereby enhancing reproductive meristem activity to produce more inflorescence branches that increase grain number per panicle [28]. Additionally, *Large Panicle* (*LP*) and *Erect Panicle 3* (*EP3*), which encode an F-Box protein located in the endoplasmic reticulum, can be used as a subunit of E3 ubiquitin ligase to regulate the expression of *OsCKX2*. Protein degradation mediated by *LP* may control CK metabolism in rice [29,30]. In addition, the expression of *OsCKX2* can also be downregulated by *Dense and Erect Panicle 1* (*DEP1*), which can be upregulated by *Ideal Plant Architecture 1* (*IPA11*) [31]. This locus is a main QTL that controls rice yield, and the coded product is homologous to the keratin 5-4 family. This allele increased the activity of rice meristem by decreasing the expression level of *OsCKX2*, resulting in shorter panicle length and panicle neck node and increased grain density. Finally, rice yield was increased by 15–20% [32,33].

Most current studies focus on the number of spikelets or size of the panicle, while studies on rice branch elongation are very limited. As a major QTL controlling yield traits of rice, mutations at the site of the dominant allele of *DEP1* result in dense panicles by reducing the length of the panicle neck, i.e., in gain-of-function mutants [32,33].

23 September 2023 23:24:08

Researchers found that the *Dense and Erect Panicle 2* (*DEP2*) mutants had erect panicles because of impaired rapid elongation of PB, SB, and rachis [34]. The erect and dense panicle genes *DEP2*, *Erect Panicle 3* (*EP2*), and *Small and Round Seed 1* (*SRS1*) are in the same locus [34-36]. In the mutant, the plant was compact and the panicle became upright, but there was no significant change in yield. Research showed that the mutation did not change the formation of rice panicle meristem primordia, but affected rachis and branch elongation; mutant stems were thick and had more vascular bundles. *Short Panicle 1* (*SP1*) participates in the regulation of rice panicle length. The mutant *sp1* still presented early young spike meristem development, but during this process the branches could not extend normally, resulting in delayed development and even degeneration of PBs and panicle shortening. Gene *SP1* is highly expressed in the phloem of the young panicle and encodes one polypeptide transporter located on the plasma membrane [37]. The *OsLiguleless 1* (*OsLG1*) mutant cannot produce panicle pulvinus owing to changes in cell morphology at the panicle ligule, which results in dense panicles in domesticated rice cultivars [38,39].

A summary of the genes involved in panicle development is shown in Figure 2. Studies on the genes described above have greatly enhanced our understanding of the genetic and molecular regulation of panicle development, but further studies are needed to comprehensively elucidate panicle development mechanisms.

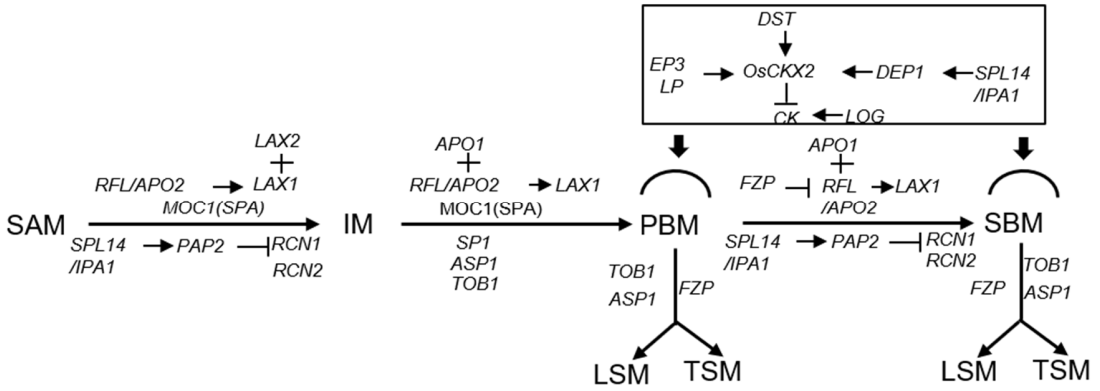

FIGURE 2. A schematic representation of genes involved in panicle formation. SAM, shoot apical meristem; IM, inflorescence meristem; PBM, primary branch meristem; SBM, secondary branch meristem; TSM, terminal spikelets meristem; LSM, lateral spikelets meristem

COORDINATED REGULATION OF PANICLE BRANCHES AND TILLERS

Tiller and panicle branches are lateral organs formed during the vegetative and reproductive phases, respectively. They both arise from SAM and involve apical growth and branching, and thus are likely regulated by common molecular mechanisms and coordinately altered in some cases. Based on the results of previous studies, the formation of tiller and panicle branches involves diverse genes with various biological functions. For instance, *LAX1* and *Monoculm 1* (*MOC1*) regulate tillers and panicle branches by generating AMs. Mutations in either gene result in a large decrease in the number of tiller and panicle branches [6,40], and changes in these numbers are consistent when regulated by *LAX1* and *MOC1*. Mutations in *LAX2* lead to a decrease in tiller number and a lack of panicle lateral branches, except for PBs [8]. The expression of RFL is regulated spatially and temporally during the development of tiller axillary primordia and panicle branch primordia, and is required for the formation of tillers and panicle branches [9].

However, changes in tiller and panicle branch numbers are not always consistent. For example, *OsCKX2*, *SP1*, and *DEP1* mutations changed panicle branch numbers but not tiller number. In some cases, the opposite results are observed, such as a reduction in tillers and increased panicle branching in *NIL-ipa1* plants [31]. Some studies on hormone related genes, such as *OsCKX2* and *Dwarf27* (*D27*) or *Dwarf53* (*D53*) [27,41,42], suggested that the temporal and spatial regulation of tiller and panicle branching might be accomplished by different genes. These studies indicate that rice panicle development during the tillering and reproductive stages might be regulated by distinct mechanisms.

23 September 2023 23:24:08

EPIGENETIC REGULATION OF PANICLE DEVELOPMENT

In addition to the genetic regulatory mechanism described above, epigenetic regulation, including post-transcriptional regulation mechanisms, is very important for understanding the progress of panicle development. The first study to report that panicle development is regulated by post-transcriptional regulation also reported that *OsSPL14/IPA1* promoted panicle primary branching and that it is regulated by *OsmicroRNA156* [14,15]. Subsequent studies showed that *SPL*, *PAP2,* and *RCN1* regulate rice tiller and panicle branching via *OsmicroRNA156, OsmicroRNA529* and *OsmicroRNA172* [17]. Locus *OsSPL14*/*IPA1* encodes a key transcription factor with pleiotropic effects on the regulation of rice plant architecture, and *IPA1* expression is controlled at the posttranscriptional level by *OsmicroRNA156* and *OsmicroRNA529* [14,15]. Recently, the *qWS8/ipa1-2D* locus was found to be associated with reduced DNA methylation and a more open chromatin state at the *IPA1* promoter, thus alleviating epigenetic repression of *IPA1* through nearby heterochromatin [43]. A recent study showed that the E3 ligase IPA1 Interacting Protein 1 (IPI1) interacts with IPA1, promotes differential polyubiquitination and degradation of IPA1 in different tissues, and consequently alters plant architecture. In panicles, the IPA1 complex is tagged by a K48-linked polyubiquitin chain, but in shoot apexes it is tagged by a K63-linked polyubiquitin chain. Therefore, the differential polyubiquitination of K48 or K63 promoted by IPI1 seems to lead to different fates of IPA1 in different tissues, resulting in fine and precise regulation of rice plant architecture [44].

The expression of *OsLG1,* which regulates rice ligule development in domesticated rice cultivars, was reported to result in compact panicle architecture and is down-regulated by DNA methylation in the promoter region of *OsLG1* [38,39]. Using genome-wide analysis, we also found that the H3K27me3/H3K4me3 ratio was a main factor responsible for the differential expression of many genes regulating growth and development during the vegetative to reproductive transition. Loss-of-function of the H3K4 demethylase gene *Jumonji703* (*JMJ703*) and the H3K27 methylase gene *Set Domain Group711* (*SDG711*) lead to reduced panicle size with lower numbers of branches and spikelets per panicle. Many genes essential for panicle development such as *OsCKX2* are regulated by *JMJ703* and *SDG711* [45]. Several DNA methyltransferases, histone acetylases/deacetylases, histone methylases/demethylases, and chromatin modification factors have been identified and characterized in rice. Loss-of-function mutations of these genes result in defects in plant development, including in panicle development [46,47].

These results indicate that epigenetic regulatory mechanisms are also very important for understanding the progress of panicle development, although the mechanism of epigenetic regulation requires further evaluation.

INVOLVEMENT OF PLANT HORMONES IN PANICLE DEVELOPMENT

Hormones are important factors in plant development regulation. An endogenous hormone that regulates branching primordia generation and elongation mainly controls the plant type. The roles of auxin, CK, and strigolactones in the branching primordium have been widely studied, and the role of CK has been described in detail.

In the reproductive meristem of Gramineae, auxin regulates AM formation and outward growth by controlling cellular polarity and cell elongation. *Oryza sativa PINOID* (*OsPID*) and *Plant Architecture and Yield 1* (*PAY1*) can affect rice branching formation by regulating the polar transport of auxin, which in turn affects the differentiation of AMs in rice inflorescence [48,49]. In addition, *LAX1*, which participates in the initiation and maintenance of the AM, is necessary for the auxin signaling pathway during the reproductive period of Gramineae [5]. Gene *ASP1* is also involved in auxin-mediated inflorescence development, and *asp1* mutants exhibit multiple defects associated with auxin; in particular, branching and spikelet number are reduced resulting in phenotypically abnormal spikelets. Although the role of *ASP1* in the auxin signaling pathway is unclear, the response of the *asp1* mutant to auxin is weak [19].

Strigolactones are recently identified plant hormones that inhibit plant branch elongation. Strigolactones such as D3, D14, and D27 are mostly associated with tiller development [41,50,51]. Recent studies showed that D53, a key repressor of the strigolactone signaling pathway, interacts with IPA1 *in vivo* and *in vitro* and suppresses the transcriptional activation of IPA1, which regulates many important phenotypes in rice, such as tiller number, plant height, and panicle morphology [42]. However, it remains unclear whether important hormones controlling branching are responsible for regulating rice panicle development or not.

The studies described above showed that nearly all plant development stages are regulated by complex networks of internal developmental signals, photoperiod, hormones, and external environmental, which overlap each other but are partly independent of each other.

23 September 2023 23:24:08

CONCLUSION

Regulation of plant development is complex and orderly, and most genes and pathways control more than one biological trait. While the roles of individual genes or pathways have been examined, how they interact to form a network and co-regulate different development processes requires further examination. Albeit the substantial progress made in the past few decades regarding the genes and pathways regulating rice panicle development, the specific mechanisms underlying them are still unclear.

Many gaps remain in understanding the molecular mechanisms that regulate yield traits and yield improvement. First, although many genes related to panicle development have been cloned, the sources of most of these genes are mutants; these mutant traits have negative agronomic characteristics, and thus these mutants cannot be directly applied in agricultural production to increase production. Second, there are differences between the actual cultivars and sequenced varieties, and the useful genes identified in the reference variety are not well approved in the commercialized varieties. Third, the complicated regulation of plant development resulted in many genes/QTLs originating pleiotropic effects and playing roles in diverse developmental processes, leading to morphological changes that exhibit different traits. Previous studies showed that yields are likely controlled by QTLs rather than by individual genes.

In recent years, researchers have developed strategies for detecting favorable allelic variations with potential applications in breeding. Currently, there are two main methods for obtaining variation resources: natural variation and artificial mutation. For natural variation, it is necessary to expand the examination of related germplasm resources, and there might be higher quality and richer allelic variation in some local breeds than in widespread breeds. With the continuous development of modern biotechnology, genome oriented editing technologies have been widely used in basic science, human gene therapy, and crop genetics and breeding. Zinc-finger nucleases (ZFNs) and transcription activator-like effector nucleases (TALENs) for genome editing enable scientists to accurately change genomes. The clustered regularly interspaced short palindromic repeats/associated protein-9 nuclease (CRISPR/Cas9) developed in recent years is directed by RNA-oriented editing technology. Like ZFNs and TALENs, the CRISPR/Cas9 system uses an engineered nuclease to generate double-strand breaks (DSBs) on the targeted DNA site, and subsequently stimulates cellular DNA repair mechanisms by exploiting the non-homologous end joining (NHEJ) or the homology-directed repair (HDR) pathways to generate small insertions/deletions/genome modifications. The CRISPR/Cas9 technology allows researchers to perform targeted mutagenesis on target genes of different crops, precisely and easily changing the sequences and functions of particular genes at exact chromosomal locations in different plant genomes. Because the CRISPR/Cas9 genome editing system is based on RNA-guided engineered nucleases, it is easier to manipulate than ZFNs and TALENs technologies. Furthermore, CRISPR/Cas9 can introduce DSBs at multiple sites. The potential of multiplexing provides practical advantages over ZFNs and TALENs technologies, as multiple target genes in the same pathway can be edited simultaneously. Unlike genetic modification, CRISPR/Cas9 generates phenotypic variation that is indistinguishable from that obtained through natural means or conventional mutagenesis. Due to the practical advantages of CRISPR/Cas9 over other genome editing technologies, it establishes a prosperous outlook in gene discovery and trait development in crop genetic improvement and breeding studies.

Additionally, rather than isolating individual genes by mutant screening, more effective methods are required for identifying useful QTLs. High-throughput sequencing and genome-wide association mapping are powerful tools for identifying QTLs by using single-nucleotide polymorphisms as molecular genetic markers to perform genome-wide association analysis (GWAS) of diverse germplasms. Regulation networks controlling rice consumption and cooking quality have been systematically dissected by GWAS [52]. These studies are also expected to identify multiple candidate genes coding for rice yield-related traits to develop elite cultivars [53].

In addition, natural variations in DNA methylation have been observed between rice cultivars and wild varieties [54]. Similarly, the frequency of epigenetic variations caused by DNA methylation variation is higher than that observed in wild-type sequences. Variation in the epigenome produces some epigenetic alleles that are stably inherited [55]. For example, differences in the expression of *OsSPL14* caused by DNA methylation lead to variations in the number of spikelets per panicle between different varieties of rice, and this type of gene expression and phenotypic variation caused by variations in epigenetic modification is stably inherited [15]. Abundant trait variations in diverse rice cultivars related to epigenomic variations, which have accumulated during the long history of domestication selection and rice evolution, provide an opportunity for studying crop epigenetics. According to the characteristics of rice, epigenome-wide association studies using DNA methylation as a molecular epigenetic marker [56] in diverse germplasms can also be used to increase rice yield while searching for epigenetic QTLs.

23 September 2023 23:24:08

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REFERENCES

1 T. Sakamoto and M. Matsuoka, Generating high-yielding varieties by genetic manipulation of plant architecture. Current opinion in biotechnology **15**, 144-147 (2004).
2 Y. Wang and J. Li, Rice, rising. Nature genetics **40**, 1273-1275 (2008).
3 Q. Zhang, Strategies for developing Green Super Rice. Proceedings of the National Academy of Sciences of the United States of America **104**, 16402-16409 (2007).
4 T. Sakamoto, and M. Matsuoka, Identifying and exploiting grain yield genes in rice. Current opinion in plant biology **11**, 209-214 (2008).
5 M. Komatsu, and M. Maekawa, K. Shimamoto, and J. Kyozuka, The LAX1 and FRIZZY PANICLE 2 genes determine the inflorescence architecture of rice by controlling rachis-branch and spikelet development. Developmental biology **231**, 364-373 (2001).
6 K. Komatsu, M. Maekawa, S. Ujiie, LAX and SPA: major regulators of shoot branching in rice. Proceedings of the National Academy of Sciences of the United States of America **100**, 11765-11770 (2003).
7 T. Oikawa, and J. Kyozuka, Two-Step Regulation of LAX PANICLE1 Protein Accumulation in Axillary Meristem Formation in Rice. The Plant cell **21**, 1095-1108 (2009).
8 H. Tabuchi, and Y. Zhang, and S. Hattori, LAX PANICLE2 of rice encodes a novel nuclear protein and regulates the formation of axillary meristems. The Plant cell **23**, 3276-3287 (2011).
9 N. N. Rao, and K. Prasad, and P. R. Kumar, and U. Vijayraghavan, Distinct regulatory role for RFL, the rice LFY homolog, in determining flowering time and plant architecture. Proceedings of the National Academy of Sciences of the United States of America **105**, 3646-3651 (2008).
10 K. Ikeda, and M. Ito, N. Nagasawa, J. Kyozuka, and Y. Nagato, Rice ABERRANT PANICLE ORGANIZATION 1, encoding an F-box protein, regulates meristem fate. The Plant journal : for cell and molecular biology **51**, 1030-1040 (2007).
11 K. Ikeda-Kawakatsu, M. Maekawa, T. Izawa, J. Itoh, and Y. Nagato, ABERRANT PANICLE ORGANIZATION 2/RFL, the rice ortholog of Arabidopsis LEAFY, suppresses the transition from inflorescence meristem to floral meristem through interaction with APO1. The Plant journal : for cell and molecular biology **69**, 168-180 (2012).
12 M. Komatsu, A. Chujo, Y. Nagato, K. Shimamoto, and J. Kyozuka, FRIZZY PANICLE is required to prevent the formation of axillary meristems and to establish floral meristem identity in rice spikelets. Development **130**, 3841-3850 (2003).
13 X. Bai, Y. Huang, and D. Mao, Regulatory role of FZP in the determination of panicle branching and spikelet formation in rice. Scientific reports **6**, 19022 (2016).
14 Y. Jiao, Y. Wang, and D. Xue, Regulation of OsSPL14 by OsmiR156 defines ideal plant architecture in rice. Nature genetics **42**, 541-544 (2010).
15 K. Miura, M. Ikeda, and A. Matsubara, OsSPL14 promotes panicle branching and higher grain productivity in rice. Nature genetics **42**, 545-549 (2010).
16 K. Kobayashi, M. Maekawa, A. Miyao, H. Hirochika, and J. Kyozuka, PANICLE PHYTOMER2 (PAP2), encoding a SEPALLATA subfamily MADS-box protein, positively controls spikelet meristem identity in rice. Plant & cell physiology **51**, 47-57 (2010).
17 L. Wang, S. Sun, and J. Jin, Coordinated regulation of vegetative and reproductive branching in rice. Proceedings of the National Academy of Sciences of the United States of America **112**, 15504-15509 (2015).
18 M. Nakagawa, K. Shimamoto, and J. Kyozuka, Overexpression of RCN1 and RCN2, rice TERMINAL FLOWER 1/CENTRORADIALIS homologs, confers delay of phase transition and altered panicle morphology in rice. The Plant journal : for cell and molecular biology **29**, 743-750 (2002).
19 A. Yoshida, Y. Ohmori, H. Kitano, F. Taguchi-Shiobara, and H. Y. Hirano, ABERRANT SPIKELET AND PANICLE1, encoding a TOPLESS-related transcriptional co-repressor, is involved in the regulation of meristem fate in rice. The Plant Journal **70**, 327-339 (2012).

23 September 2023 23:24:08

20 W. Tanaka, T. Toriba, and H. Y. Hirano, Three TOB1-related YABBY genes are required to maintain proper function of the spikelet and branch meristems in rice. New Phytologist **215**, 825-839 (2017).
21 M. R. Tucker, and T. Laux, Connecting the paths in plant stem cell regulation. Trends in cell biology **17**, 403-410 (2007).
22 B. Veit, Hormone mediated regulation of the shoot apical meristem. Plant molecular biology **69**, 397-408 (2009).
23 T. Werner, and V. Motyka, M. Strnad and T. Schmulling, Regulation of plant growth by cytokinin. Proceedings of the National Academy of Sciences of the United States of America **98**, 10487-10492 (2001).
24 T. Werner, V. Motyka, and V. Laucou, Cytokinin-deficient transgenic Arabidopsis plants show multiple developmental alterations indicating opposite functions of cytokinins in the regulation of shoot and root meristem activity. The Plant cell **15**, 2532-2550 (2003).
25 M. Riefler, O. Novak, M. Strnad, and T. Schmulling, Arabidopsis cytokinin receptor mutants reveal functions in shoot growth, leaf senescence, seed size, germination, root development, and cytokinin metabolism. The Plant cell **18**, 40-54 (2006).
26 T. Kurakawa, N. Ueda, and M. Maekawa, Direct control of shoot meristem activity by a cytokinin-activating enzyme. Nature **445**, 652-655 (2007).
27 M. Ashikari, H. Sakakibara, S. Lin, *et al.* Cytokinin oxidase regulates rice grain production. Science **309**, 741-745 (2005).
28 S. Li, B. Zhao, D. Yuan, *et al.* Rice zinc finger protein DST enhances grain production through controlling Gn1a/OsCKX2 expression. Proceedings of the National Academy of Sciences of the United States of America **110**, 3167-3172 (2013).
29 M. Li, D. Tang, K. Wang, *et al.* Mutations in the F-box gene LARGER PANICLE improve the panicle architecture and enhance the grain yield in rice. Plant biotechnology journal **9**, 1002-1013 (2011).
30 H. Yu, E. H. Murchie, Z. H. González-Carranza, K. A. Pyke, and J. Roberts, A. Decreased photosynthesis in the erect panicle 3 (ep3) mutant of rice is associated with reduced stomatal conductance and attenuated guard cell development. Journal of experimental botany **66**, 1543-1552 (2015).
31 Z. Lu, H. Yu, G. Xiong, *et al.* Genome-Wide Binding Analysis of the Transcription Activator IDEAL PLANT ARCHITECTURE1 Reveals a Complex Network Regulating Rice Plant Architecture. The Plant cell **25**, 3743-3759 (2013).
32 X. Huang, Q. Qian, Z. Liu, *et al.* Natural variation at the DEP1 locus enhances grain yield in rice. Nature genetics **41**, 494-497 (2009).
33 Y. Zhou, J. Zhu, Z. Li, *et al.* Deletion in a quantitative trait gene qPE9-1 associated with panicle erectness improves plant architecture during rice domestication. Genetics **183**, 315-324 (2009).
34 F. Li, W. Liu, J. Tang, *et al.* Rice DENSE AND ERECT PANICLE 2 is essential for determining panicle outgrowth and elongation. Cell research **20**, 838-849 (2010).
35 Y. Abe, K. Mieda, T. Ando, *et al.* The SMALL AND ROUND SEED1 (SRS1/ DEP2) gene is involved in the regulation of seed size in rice. . Genes & genetic systems, **85**, 327–339 (2010).
36 K. Zhu, D. Tang, C. Yan, *et al.* Erect panicle2 encodes a novel protein that regulates panicle erectness in indica rice. Genetics **184**, 343-350 (2010).
37 S. Li, Q. Qian, Z. Fu, *et al.* Short panicle1 encodes a putative PTR family transporter and determines rice panicle size. The Plant journal : for cell and molecular biology **58**, 592-605 (2009).
38 T. Ishii, K. Numaguchi, K. Miura, *et al.* OsLG1 regulates a closed panicle trait in domesticated rice. Nature genetics **45**, 462-465, 465e461-462 (2013).
39 Z. Zhu, L. Tan, Y. Fu, *et al.* Genetic control of inflorescence architecture during rice domestication. Nature communications **4**, 2200 (2013).
40 X. Li, Q. Qian, Z. Fu, *et al.* Control of tillering in rice. Nature **422**, 618-621 (2003).
41 H. Lin, R. Wang, Q. Qian, *et al.* DWARF27, an Iron-Containing Protein Required for the Biosynthesis of Strigolactones, Regulates Rice Tiller Bud Outgrowth. The Plant Cell Online **21**, 1512-1525 (2009).
42 X. Song, Z. Lu, H. Yu, *et al.* IPA1 functions as a downstream transcription factor repressed by D53 in strigolactone signaling in rice. Cell research **27**, 1128-1141 (2017).
43 L. Zhang, H. Yu, B. Ma, *et al.* A natural tandem array alleviates epigenetic repression of IPA1 and leads to superior yielding rice. Nature communications, **8**, 14789 (2017).
44 J. Wang, H. Yu, G. Xiong, *et al.* Tissue-Specific Ubiquitination by IPA1 INTERACTING PROTEIN1 Modulates IPA1 Protein Levels to Regulate Plant Architecture in Rice. The Plant cell **29**, 697-707 (2017).
45 X. Liu, S. Zhou, W. Wang, *et al.* Regulation of histone methylation and reprogramming of gene expression in the rice inflorescence meristem. The Plant cell **27**, 1428-1444 (2015).

23 September 2023 23:24:08

46 X. Chen, and D. X. Zhou, Rice epigenomics and epigenetics: challenges and opportunities. Current opinion in plant biology **16**, 164-169 (2013).
47 S. Moritoh, C. H. Eun, A. Ono, *et al.* Targeted disruption of an orthologue of DOMAINS REARRANGED METHYLASE 2, OsDRM2, impairs the growth of rice plants by abnormal DNA methylation. The Plant journal : for cell and molecular biology **71**, 85-98 (2012).
48 L. Zhao, L. Tan, Z. Zhu, *et al.* PAY1improves plant architecture and enhances grain yield in rice. The Plant Journal **83**, 528-536 (2015).
49 Y. Morita, and J. Kyozuka, Characterization of OsPID, the Rice Ortholog of PINOID, and its Possible Involvement in the Control of Polar Auxin Transport. Plant and Cell Physiology **48**, 540-549 (2007).
50 T. Arite, M. Umehara, S. Ishikawa, *et al.* d14, a Strigolactone-Insensitive Mutant of Rice, Shows an Accelerated Outgrowth of Tillers. Plant and Cell Physiology **50**, 1416-1424 (2009).
51 S. Ishikawa, Suppression of Tiller Bud Activity in Tillering Dwarf Mutants of Rice. Plant and Cell Physiology **46**, 79-86 (2005).
52 Z. Tian, Q. Qian, Q. Liu, *et al.* Allelic diversities in rice starch biosynthesis lead to a diverse array of rice eating and cooking qualities. Proceedings of the National Academy of Sciences of the United States of America **106**, 21760-21765 (2009).
53 S. Crowell, P. Korniliev, A. Falcao, *et al.* Genome-wide association and high-resolution phenotyping link Oryza sativa panicle traits to numerous trait-specific QTL clusters. Nature communications **7**, 10527 (2016).
54 X. Li, J. Zhu, F. Hu, *et al.* Single-base resolution maps of cultivated and wild rice methylomes and regulatory roles of DNA methylation in plant gene expression. BMC genomics **13**, 300 (2012).
55 E. J. Richards, Natural epigenetic variation in plant species: a view from the field. Current opinion in plant biology **14**, 204-209 (2011).
56 A. Y. Chu, A. Tin, P. Schlosser, *et al.* Epigenome-wide association studies identify DNA methylation associated with kidney function. Nature communications **8**, 1286 (2017).

23 September 2023 23:24:08