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Review

Tillering and panicle branching genes in rice

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ABSTRACT

Rice (*Oryza sativa* L.) is one of the most important staple food crops in the world, and rice tillering and panicle branching are important traits determining grain yield. Since the gene *MONOCULM 1* (*MOC 1*) was first characterized as a key regulator in controlling rice tillering and branching, great progress has been achieved in identifying important genes associated with grain yield, elucidating the genetic basis of yield-related traits. Some of these important genes were shown to be applicable for molecular breeding of high-yielding rice. This review focuses on recent advances, with emphasis on rice tillering and panicle branching genes, and their regulatory networks.

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Contents

1. Introduction

Rice is one of the most important grain crops and feeds nearly half of the global population. In the twenty-first century, the world faces a serious challenge in that agricultural land area has sharply decreased in contrast to a population explosion. To solve the crisis of food shortage, it is urgent to improve crop productivity especially for rice. With the accomplishments of the Rice Genome Project, increasingly genes and QTLs (quantitative trait loci) which are responsible for various important agronomic traits have been identified. Based on its progress, knowledge of the molecular biology provides a series of methods that can be applied to feasible breeding programs aimed at improving rice productivity.

Rice tillering is an important agronomic trait, as tiller number per plant determines panicle number, which is a key component of rice grain yield (Yan et al., 1998). The rice panicle branching in valid tillers determines the number of panicle-bearing tillers and grain number per panicle. Rice tillering and panicle branching have been well investigated over the past several years due to their agronomic importance (Wang and Li, 2011). Recently, there was a major breakthrough in elucidating the molecular mechanisms underlying rice tillering and panicle branching. Especially with molecular marker-facilitated mapping of QTLs, several QTLs or genes associated with these important agronomic traits have been detected or identified. In this review, we summarize recent progress in the exploration and functional declaration of genes involved in the direct formation of grain yield by tillering and panicle branching.

2. Rice tillering genes

Tillering is not only one of the most important factors related to rice yield but also a central subject concerning plant architecture being

Abbreviations: QTLs, quantitative trait loci; *MOC 1*, *MONOCULM 1*; LS/LAS, lateral suppressor; AMs, axillary meristems; tad1, tillering and dwarf 1; te, tiller enhancer; APC/C, anaphase promoting complex/cyclosome; lax, *Lax Panicle*; SPA, *SMALL PANICLE*; *TB1*, *TEOSINTE BRANCHED1*; MAX, MORE AUXILIARY GROWTH; *D14*, *Dwarf 14*; SL, strigolactone; *FC1*, *FINE CULM1*; BRs, brassinosteroids; *BIN2*, *BRASSINOSTEROID-INSENSITIVE 2*; IPA1, *IDEAL PLANT ARCHITECTURE1*; WFP, *Wealthy Farmer's Panicle*; OsSPL14, SQUAMOSA PROMOTER BINDING PROTEIN-LIKE14; DEP, DENSE AND ERECT PANICLE; UFO, UNUSUAL FLORAL ORGANS; APO1, *ABERRANT PANICLE ORGANIZATION 1*; SNB, *SUPERNUMERARY BRACT*; IDS1, *INDETERMINATE SPIKELET1*; sp1, *SHORT PANICLE 1*; LRR, leucine-rich repeat.

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discussed in biology. For the past several decades, scientists have been trying to elucidate and characterize QTLs for tiller number. The first gene identified as a key regulator controlling rice tillering and branching was *MOC1* (Li et al., 2003), an ortholog of lateral suppressor (*LS*/*LAS*) gene from tomato (*Solanum lycopersicum*) (Schumacher et al., 1999) and *Arabidopsis thaliana* (Greb et al., 2003). *MOC1* encodes a transcriptional regulator, belongs to the GRAS (*GAI*, *RGA* and *SCR*) family (Pysh et al., 1999), which mainly expressed in the axillary buds and controls initiation and outgrowth of axillary meristems (AMs) at both vegetative and reproductive stages. As a result, the rice mutant *moc1* (*MONOCULM 1*) almost completely loses tillering ability, and has a characteristic monoculm, which revealed that MOC1 functions as a positive regulator for rice tillers and panicle branches. Recently, two novel genes, *TAD1* and *TE*, were identified to coexpress with *MOC1* in the axil of leaves, which conferred rice tillering and branching control with *MOC1*. *TAD1* (Xu et al., 2012) was isolated from the *tad1* (*tillering and dwarf 1*) mutant, which shows increased tillers and reduced plant height. *TE* (Lin et al., 2012) was isolated from the *te* (*tiller enhancer*) mutant, which displays a drastically increased tiller number. The two genes work upstream of *MOC1*, and encode a rice homolog of Cdh1 (Li et al., 2009) that functions as a co-activator or activator of APC/C (anaphase promoting complex/cyclosome) (Foe and Toczyski, 2011; Pines, 2011), which is a multi-subunit ubiquitin ligase. TAD1 interacts with MOC1, forms the APC/C^{TAD1} complex with OsAPC10, and functions as a co-activator of APC/C to target MOC1 for degradation in a cell-cycle-dependent manner. TE is a substrate-recognition and -binding factor of the APC/C, involved in the formation of APC/C^{TE} complex interacting with MOC1 and OsCDC27, and mediates the degradation of MOC1 by the ubiquitin-26S proteasome pathway, and reducing expression of the meristem identity gene *OSH1*. Thus, current research uncovered the underlying mechanisms involved in the APC/C–MOC1 complex (Fig. 1), the degradation of MOC1 with APC/$C^{TAD1/TE}$ in a cell-cycle-dependent manner, which regulates rice tillering pattern and finally determines grain yield (Lin et al., 2012; Xu et al., 2012).

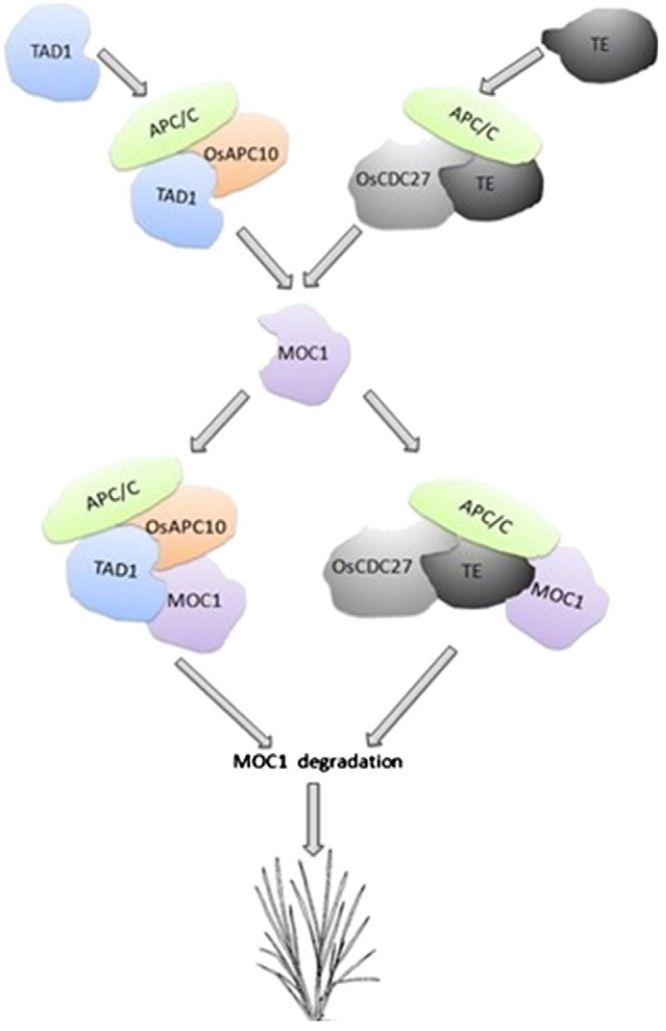

Fig. 1. A working model for rice tillering regulated by the degradation of MOC1 with APC/$C^{TAD1/TE}$.

Rice *LAX1* encodes a putative transcriptional regulator and was isolated from the *lax1* (*lax panicle 1*) mutant by positional cloning (Komatsu et al., 2003). Further study showed that *LAX1* is a regulator controlling axillary meristem initiation and/or maintenance during rice reproductive development, and functions redundantly with *SPA* (*SMALL PANICLE*) in the same genetic pathway. LAX1 may transiently accumulate in the initiating AM at the plastochron 4 stage, which strictly regulates mRNA expression and subsequent control of protein trafficking (Oikawa and Kyozuka, 2009). By map-based cloning, *LAX2* was isolated from the *lax2* (*LAX PANICLE 2*) mutant, which has a similar phenotype to *lax1* in that it lacks an AM in most of the lateral branches of the panicle, and has a reduced number of AMs at the vegetative stage. *LAX2* encodes a nuclear protein that physically interacts with LAX1, suggesting that the two LAXs may act together in regulating rice AM formation process (Tabuchi et al., 2011). So far, there is a consensus that some plant hormones, such as two classical hormones—auxins and cytokinins (Hayward et al., 2009; Leyser, 2003)—are involved in tillering and branching. Several genes acting downstream of these phytohormones have been isolated. Rice *OsTB1* was first identified based on its sequence similarity with maize (*Zea mays*) homolog *TB1* (*TEOSINTE BRANCHED1*), which is involved in lateral branching in maize. *OsTB1* encodes a putative transcription factor carrying a helix–loop–helix type of DNA-binding motif (Takeda et al., 2003). Expression of *TB1* homolog *BRC1*/*TBL1* in *Arabidopsis* hormone signaling mutants suggests that TB1 acts downstream of the auxin and MAX (MORE AUXILIARY GROWTH) pathways (Aguilar-Martinez et al., 2007; Finlayson, 2007). According to the phenotypes of *OsTB1* transgenic rice, the number of tillers and panicles were respectively reduced and increased in overexpressed and RNAi rice, demonstrating that the gene functions as a negative regulator for lateral branching in rice (Choi et al., 2012).

Recently, a rice transcription factor, OsMADS57, was reported to interact with OsTB1, and targets *D14* (*Dwarf 14*) to control the outgrowth of axillary buds (Guo et al., 2013). *D14* has been shown to participate in the strigolactone (SL) signaling pathways, to inhibit rice tillering and to be an SL receptor candidate in the branching inhibition pathway (Arite et al., 2009). By positional cloning, another gene *FC1* was identified from rice mutant *fc1* (*FINE CULM1*) with increased tillering phenotype (Minakuchi et al., 2010). *FC1* was initially reported as an ortholog of *TB1*, which is one of the major loci responsible for domestication in maize (Doebley et al., 1995, 1997; Hubbard et al., 2002). The *fc1* mutant phenotype cannot be rescued by the function of SL and its synthetic analogs as branching inhibitors, implying that proper FC1 functioning is required for SLs to inhibit bud growth, and works downstream of SLs.

From a series of rice dwarf mutants conferred with increased number of tillers, the corresponding genes were identified: *D3* (Ishikawa et al., 2005), *D17* (Booker et al., 2004), *D10* (Arite et al., 2007), *D14* (Arite et al., 2009) and *D27* (Lin et al., 2009). Although these genes have been suggested to be involved in the regulation of axillary bud outgrowth for tillering in rice—in fact, some dwarf genes function in SL biosynthesis, such as *D10*, *D27* and *D17*; and others are involved in SL perception, such as *D3* and *D14*.

The steroid hormones brassinosteroids (BRs) have also been shown to be involved in rice tillering. The phenotype of rice *dlt* (*dwarf and low tillering*) mutant is similar to BR-deficient or BR-signaling mutants in rice, which has a dwarf phenotype and reduced tiller numbers. The corresponding gene *DLT* which encodes a new member of the plant-specific GRAS family was cloned from the *dlt* mutant by map-based

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