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Review Article

OsMADS1/OsLHS1: Diversified Regulatory Functions in Ensuring Transition and Completion of Sexual Reproduction in Rice

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Sexual reproduction is a highly adopted mode of propagation in higher plants. Monocot grass species develop fertile florets on the spikelet of their inflorescences (panicle). MADS-box containing SEPALLATA proteins, together with other transcription factors play crucial role during floral meristem specification, organogenesis and meristem determinacy. Unlike four largely redundant SEP genes in *Arabidopsis,* five rice SEP genes display both redundant and non-redundant functions in controlling reproductive development. *LEAFY HULL STERILE1/OsMADS1*, member of a grass-specific *LOFSEP* clade of rice SEP gene family, is required for specification and development of a fertile floret on the spikelet meristem. *OsMADS1* irreversibly promotes spikelet to floret transition by specifying floret meristem identity and repressing spikelet identity. It also suppresses reversion of floret meristem to shoot meristem fate. During later stages, while *OsMADS1* maintains floret meristem functions, it also controls floret organ specification and differentiation and determinacy of floret meristem. These diverse functions of *OsMADS1* are brought by its genetic and physical interactions with various other genetic regulators and forming higher order complexes at different developmental stages. Thus, all functional data in corroboration with estimated evolutionary divergence time scale of *OsMADS1* sub-clade suggest that *OsMADS1* is co-evolved with grasses and as a key regulator of rice sexual reproductive habit, it has not only retained its conserved functions but also has acquired some species-specific functions.

Keywords: Panicle; Meristem; MADS; SEPALLATA; Spikelet; Floret; Determinacy

Introduction

Sexual reproduction is a major mode of propagation in angiosperms and is widely believed to have evolved from asexual reproduction (Wang *et al.,* 2010). Reproductive stage in plant begins with a phase of transition through change in identity of vegetative shoot apical meristem (SAM) to inflorescence meristem (IM). The IMs next either terminate by acquiring floral meristems (FMs) identity or develop several inflorescence branch meristems (BMs) to provide higher order inflorescence branching (Prusinkiewicz *et al.*, 2007; Liu *et al.*, 2013; Pautler *et al.*, 2013, Tanaka *et al.*, 2013). Thus, inflorescence architecture in different plant species is established by differential developmental decisions at IM stage to bring various types of inflorescence (Prusinkiewicz *et al.*, 2007; Liu *et al.*, 2013).

Model dicot plant, *Arabidopsis thaliana* develops raceme-type inflorescence composed of a main indeterminate inflorescence axis bearing either a terminal flower or lateral axes with features similar to main axis at the lateral position (Prusinkiewicz *et al.*, 2007). However, in various other plant species, inflorescence architecture is relatively more complex. Monocot grass species posses a highly branched inflorescence, called panicle. In rice, panicle has a main axis (also called rachis) containing several lateral primary branches (Fig. 1B; Ikeda *et al.*, 2004). Secondary branches emerge on the primary branches and spikelets are present on both primary and secondary branches (Fig. 1B; Ikeda *et al.,* 2004; Tanaka *et al.,* 2013; Kyozuka *et al.,* 2014). A rice spikelet is considered to have three florets subtended by a pair of rudimentary glumes (Fig. 1C and 1D).

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Among these, two lower florets are sterile (also called sterile lemma or empty glumes) and only the single upper floret is fertile (Fig. 1C and 1D). Therefore, unlike in *Arabidopsis,* where FMs are directly formed either on the main or lateral inflorescence axes, in rice, various intermediate meristems are formed after reproductive transition (Fig. 1A). These meristems are for primary branches (PBMs), secondary branches (SBMs) and for the spikelets (SMs) that finally terminate into floret meristems (FMs). Apart from inflorescence architecture, flower morphology is also diversified in grass-species. *Arabidopsis* FM develops four floral organs arranged in concentric whorls; from outer to inner whorls composed of four sepals, four petals, six stamens and a carpel. The rice floret contains two bract-like structures, a lemma and a palea (sepal equivalent), a pair of fleshy lodicules (petal equivalent), six stamens and a central carpel (Fig. 1D; Kater *et al.*, 2006; Yoshida and Nagato, 2011; Hu *et al.,* 2015).

SEPALLATA MADS-box Genes are Key Players for Flower Development

Floral organ specification and patterning in an angiosperm plant are regulated by individual and combined functions of MADS-box containing transcription factors, classified into A, B, C, D and E classes (Fig. 2A; Coen and Meyerowitz, 1991; Riechmann *et al.*, 1996; Parcy *et al.*, 1998; Theissen, 2001; Krizek and Fletcher, 2005). In model dicot plant, *Arabidopsis thaliana*, four largely redundant MADS-box SEPALLATA proteins, (SEP1, 2, 3 and 4) function as co-factors with Class A, B and C factors and by forming complexes with them, they control determination of floral organ identities and also regulate determinacy of floral meristem (Pelaz *et al.*, 2000; 2001;Honma and Goto, 2001; Ditta *et al.*, 2004). The *sep1/2/3* triple mutants display floral phenotypes similar to double loss of B- and C-class functions where floral organs are homeotically converted into sepals (Pelaz *et al.*, 2000). Furthermore, C-function gene *AGAMOUS* (*AG*) fails to activate the expression of its target *SHATTERPROOF2* (*SHP2*) in carpels of triple mutants (Castillejo *et al.*, 2005).These observations indicate that SEP genes are required by ABC genes for their role in whorl-specific organ patterning. Moreover, upon loss of all four SEP genes (*sep1/2/3/4*), the floral organs are converted to leaf-

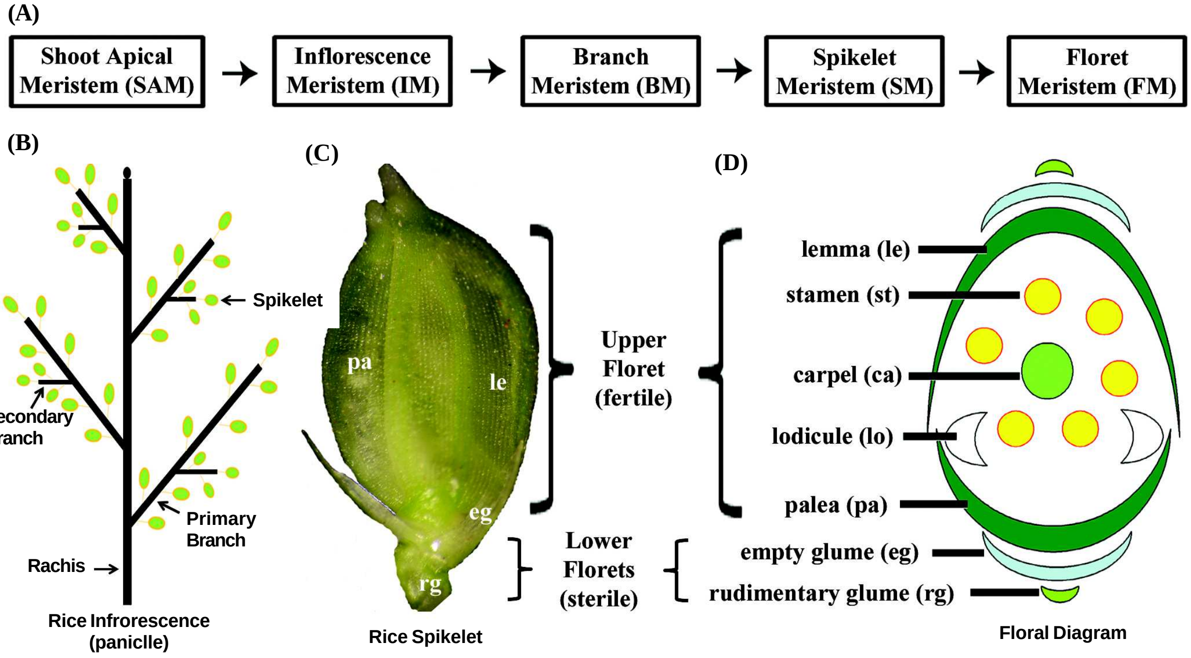

Fig. 1: Reproductive development in rice. (A) Schematic representation showing various meristem transitions during rice reproductive development. (B) Schematic diagram showing architecture of a rice inflorescence (also called panicle). (C and D) Morphology (C) and floral diagram (D) of a rice spikelet. Rudimentary glumes (rg) and empty glumes (eg) are underdeveloped sterile florets. Lemma (le) and palea (pa) enclose inner floret organs; two lodicules, six stamens and a carpel

like structure (Ditta *et al.*, 2004). Complementary observations of leaf-to-petal conversion phenotypes upon simultaneous ectopic over-expression of Class A, B and SEP genes and analysis of protein-protein interaction, further to support their pivotal role in floral organ patterning (Pelaz *et al.*, 2001; Immink *et al.*, 2009).

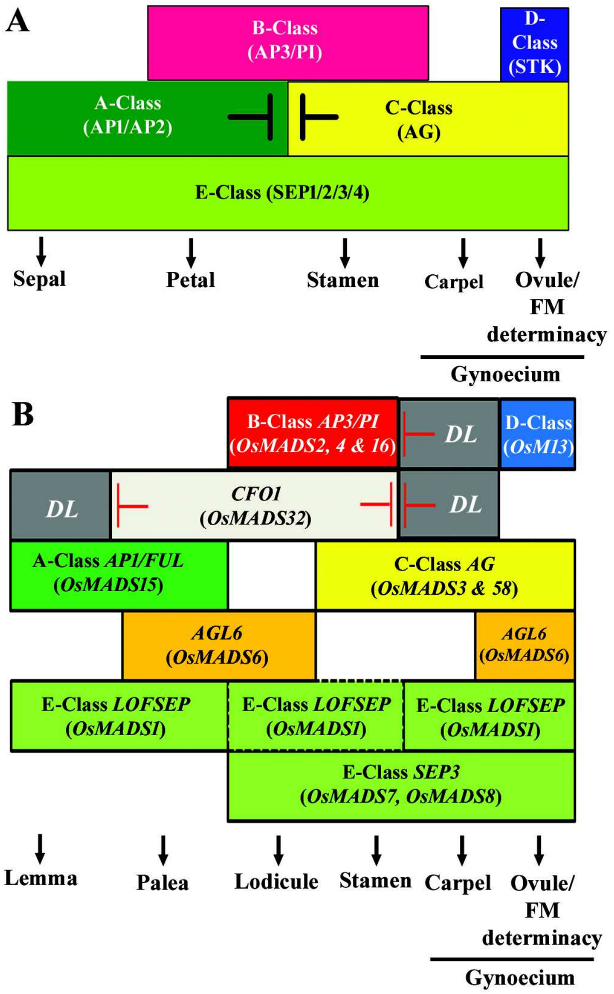

Fig. 2: Interactions and functions of genetic regulators of flower development. (A) Combinatorial action of genetic regulators of floral organ patterning and floral meristem determinacy in *Arabidopsis*. Overlapping expression and interactions of ABCDE genes regulate floral organ patterning. (B) Schematic diagram showing interactions and functions of genetic regulators of floret development in rice. Apart from conserved and diverged functions of rice ABCDE genes, other regulators such as *OsMADS6, OsMADS32* (*CFO1*) and *DL* also play role during rice floret development. Dashed box indicates a domain where gene functions non-cell autonomously (gene is not expressed but has a function)

Members of ABCDE classes have also been identified in rice and their modes of actions are conserved as well as diversified (Fig. 2B). Flower development in rice also involves some additional species-specific genetic regulators (Fig. 2B). Homologs for *SEP* genes are identified in several plant species but unlike in *Arabidopsis*, they often have discrete and species-specific roles in other plants by acquiring neo- and sub-functionalization during flower development (Kotilainen *et al.*, 2000; Uimari *et al.*, 2004; Malcomber and Kellogg, 2005; Zahn *et al.*, 2005; Cui *et al.*, 2010). *SEP* genes have experienced several gene duplications during the evolution (Malcomber and Kellogg, 2005; Zahn *et al.*, 2005). They form a clade within the phylogeny of MADS box genes that can be broadly divided into two clades; the *SEP3* clade having *AtSEP3* and the *LOFSEP* clade containing *AtSEP1, 2* and *4* (Malcomber and Kellogg, 2005), each with several subclades. Rice has five E-class genes, *LEAFY HULL STERILE1*(*LHS1*)/*OsMADS1*, *OsMADS5*, *OsMADS7/45*, *OsMADS8/24* and *PANICLE PHYTOMER 2* (*PAP2*)/*OsMADS34* that redundantly and non-redundantly ensure 'floret state' in rice (Kater *et al.*, 2006; Cui *et al.*, 2010). Of these, *OsMADS7* and *8* belonging to *SEP3* clade, have conserved and redundant functions in regulating inner floret organ development whereas others fall into grass-specific *LOFSEP* clade and have acquired species-specific novel functions (Malcomber and Kellogg, 2005; Cui *et al.*, 2010; Gao *et al.*, 2010; Kobayashi *et al.*, 2010). Simultaneous down-regulation of four E-class genes in rice (i.e. *OsMADS1*, *OsMADS5*, *OsMADS7*, and *OsMADS8*) results in a homeotic transformation of all floral organs but lemma into leaf-like organs that mimics *Arabidopsis sep1/2/3/4* quadruple mutant phenotypes, suggesting a conserved basic E-class function in rice floret organ specification and meristem determinacy (Cui *et al.*, 2010). However, unlike *Arabidopsis SEP* genes, where single mutants display either none or subtle phenotypes (Pelaz *et al.*, 2000; Ditta *et al.*, 2004), single mutants for *OsMADS1* or *OsMADS34* and *osmads1 osmads34* double mutants exhibit obvious defects during reproductive development, suggesting their redundant and non-redundant functions in controlling rice flower development (Jeon *et al.*, 2000; Prasad *et al.*, 2001, 2005; Cui *et al.*, 2010; Gao *et al.*, 2010; Kobayashi *et al.*, 2010). Among all SEP genes, *OsMADS34* has the earliest functions and controls panicle morphology by regulating spikelet meristem identity (Gao *et al.*, 2010; Kobayashi *et al.*, 2010). Similar to *Arabidopsis SEP3*, *OsMADS7* and *8* together control differentiation of floret organs such as lodicules, stamens, carpel and regulate floret meristem determinacy (Cui *et al.*, 2010). *OsMADS1* is expressed in floret meristems, lemma/palea and weakly in carpel primordia (Prasad *et al.*, 2001; 2005) and regulates the establishment of floret meristem identity, patterning of rice floret organs and determinacy of floret meristem (Jeon *et al.*, 2000; Prasad *et al.*, 2001, 2005; Agrawal *et al.*, 2005; Ohmori*et al.*, 2009; Cui *et al.*, 2010; Gao *et al.*, 2010; Li *et al.*, 2010; Wang *et al.*, 2010). The expression of *OsMADS1* is activated by jasmonic acid (JA) during spikelet development in rice (Cai *et al*., 2014). Thus, rice *SEP* genes regulate the development of all reproductive stages, such as panicle and spikelet morphology, floret meristem transition and fate determination, differentiation of floret organs and meristem determinacy (Jeon *et al.*, 2000; Prasad *et al.*, 2005; Cui *et al.*, 2010; Gao *et al.*, 2010; Kobayashi *et al.*, 2010). In this review, we will describe multiple roles of *OsMADS1* and its interactions with other genetic regulators in ensuring sexual reproduction in rice (Fig. 3).

Members of *SEP*-sister clade, *AGAMOUS-LIKE6* (*AGL6*)-*like* MADS box gene, *MOSAIC FLORAL ORGANS1* (*MFO1*)/*OsMADS6* and *OsMADS17*, also have functions similar to *OsMADS1* during rice floret development (Ohmori *et al.*, 2009; Li *et al.*, 2010; Yoshida and Nagato, 2011; Duan *et al.*, 2012). *mfo1*/*osmads6* mutant displays altered palea and lodicule identities, mosaic inner organs, defective carpel development and loses floret meristem determinacy. Down-regulation of *OsMADS17* in *mfo1-2* background further enhances *mfo1* phenotypes (Ohmori *et al.*, 2009). Genetic interaction analysis revealed that *OsMADS6* controls organ identities in the inner three whorls and meristem determinacy, redundantly with rice B-class (*OsMADS16*), C-class (*OsMADS3*and *58*) and D-class genes (*OsMADS13*) whereas it regulates identities of floral meristem and palea together with a

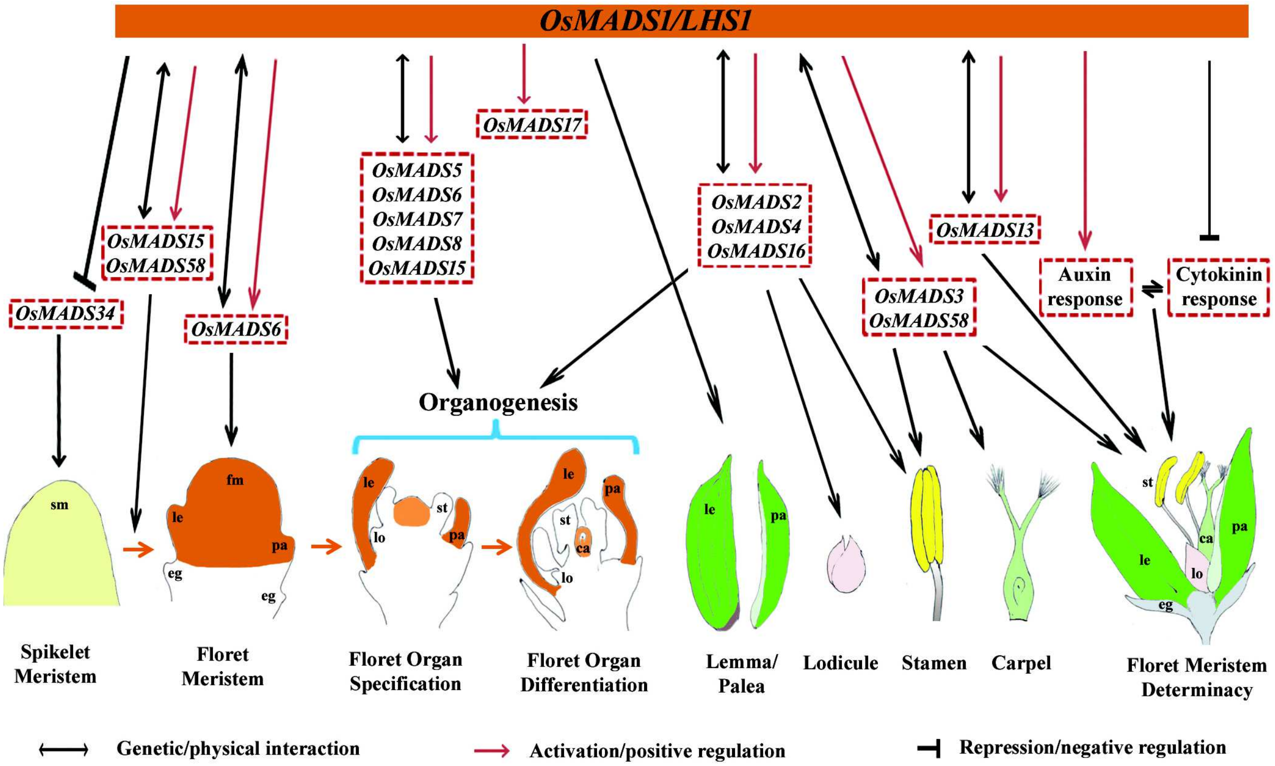

Fig. 3: ***OsMADS1*** **regulation of floret transition, organogenesis and floret meristem determinacy. A model showing physical and genetic interactions of** ***OsMADS1*** **with various genetic regulators, auxin and cytokinin signaling pathways and their regulatory functions during entire process of reproductive development in rice. sm; spikelet meristem; fm; floret meristem; eg; empty glume; le; lemma; pa; palea; lo; lodicule; st; stamen; ca; carpel**

YABBY member, *DROOPING LEAF* (Li *et al*., 2011a). Interestingly, *OsMADS6* also interacts with *OsMADS1* and they together control floret meristem establishment, organogenesis andmeristem determinacy (Ohmori *et al*., 2009; Li *et al*., 2010; Yoshida and Nagato, 2011). Moreover, a monocot-specific MADS gene, *CHIMERIC FLORAL ORGANS1/OsMADS32* also regulates floral organ identities in rice, suggesting evolution of multiple genetic regulators for floret development in grasses (Sang *et al*., 2012).

OsMADS1 Regulates Genetic Networks Required for the Spikelet-to-Floret Transition

Molecular phylogenetic analysis of MADS-box genes estimates evolutionary divergence of *OsMADS1* clade approximately 58-62 million years ago, coinciding with the divergence time-scale of grasses (~60 million years ago) and therefore, have been predicted to acquire grass-specific functions (Doyle, 1973; Prasad *et al.*, 2005; Khanday *et al.*, 2013). Within the grass species, the *LHS1* genes display heterogeneous expression pattern but their expression in the upper florets of the spikelet is conserved (Malcomber and Kellogg, 2004). *OsMADS1* is expressed only in the upper floret meristem of rice spikelet which produces fertile florets and it is completely excluded from the glumes which are vestiges of sterile lower florets (Prasad *et al*., 2001; Bommert *et al*., 2005). Loss-of *OsMADS1* functions results in a perturbed and indeterminate floret meristem identity developing glume/lemma-like repeated floret organs (Jeon *et al*., 2000; Prasad *et al*., 2005; Agrawal *et al*., 2005). This indicates that presence of *OsMADS1* in upper floret meristem is needed to initiate developmental programs to produce fertile florets and in its absence, upper floret meristem also takes identity similar to the lower florets. This is also supported by the fact that, ectopic over-expression of *OsMADS1* causes a homeotic conversion of outer glumes into lemma-like organs (Jeon *et al*., 2000; Prasad *et al*., 2001), further confirming that *OsMADS1* is sufficient to initiate upper floret-specific developmental program ectopically in sterile florets.

A regulatory relationship between *OsMADS1* and *OsMADS34* plays an important role during spikelet-to-floret transition. *OsMADS34* is expressed in developing inflorescences and is required for spikelet meristem identity on rachis branches in rice (Gao *et al*., 2010; Kobayashi *et al*., 2010). Loss-of-function mutants of *osmads34/panicle phytomer2-1* display decreased and abnormal spikelets with elongated glumes and transformation of early spikelets into inflorescence branches (Gao *et al*., 2010; Kobayashi *et al*., 2010). *OsMADS1* is expressed slightly later than *OsMADS34* and directly represses the expression of *OsMADS34* in developing panicles (Gao *et al*., 2010; Kobayashi *et al*., 2010; Khanday *et al*., 2013). Thus, *OsMADS34* controls branch-to-spikelet transition and *OsMADS1* functions spikelet-to-floret transition. In addition to their exclusive functions in meristem transitions, they together regulate floret organogenesis in rice as consistent with *osmads1 osmads34* double mutant phenotypes (Gao *et al*., 2010; Kobayashi *et al*., 2010). *OsMADS1* also interacts with rice C-function gene, *OsMADS58* and controls spikelet meristem reversion (Hu *et al*., 2015), further confirming that *OsMADS1* functions as a repressor of spikelet meristem and activator of floret meristem identity.

OsMADS1 Suppresses Reversion from Sexual-to-Asexual Reproduction Habit

Distinct functions of *OsMADS1* in different tissues or at different developmental stages are brought about by its genetic and physical interactions with different regulators. After ensuring spikelet to floret meristem transition, *OsMADS1* also suppresses its reversion to shoot meristem fate (Wang *et al*., 2010). Genetic analysis of three naturally occurring mutants, *degenerativepalea* (*dep*), *abnormal floralorgans* (*afo*) and *phoenix* (*pho*) demonstrate a cooperative role of *OsMADS1* and *OsMADS15* in establishing sexual reproductive habits of rice (Wang *et al*., 2010). *Dep* mutant has a single point mutation in the coding region of an *AP1/FUL*-like gene, *OsMADS15* whereas *afo* has an epigenetic mutation at *OsMADS1* locus. *pho* is a double mutant for both of these alleles. *Dep* mutants exhibit unstable pseudo vivipary occasionally under certain environmental condition where new shoots emerged from the floret organs. However, *pho* mutants produce stable pseudovivipary where all florets are always replaced by young plantlets in mutant panicles (Wang *et al*., 2010). Interestingly, these plantlets have capability to produce roots and tillers when transferred to field and propagate through asexual mode in next generation suggesting that the double mutant has completely changed its reproductive habits from sexual to asexual mode. In their cooperative functions of inhibiting pseudovivipary in rice, *OsMADS1* promotes floret meristem specifications whereas *OsMADS15* inhibits SAM formation (Wang *et al.*, 2010).

Further, *OsMADS15* also genetically interacts with *OsMADS34/PAP2* in early developmental stages and regulates transition from SAM to IM, redundantly with other *AP1/FUL*-like genes, *OsMADS14* and *18* (Kobayashi *et al.*, 2012). IM identity is established normally in single mutants of these genes but in strong *MADS14;15;18i/pap2-1* quadruple knockdown lines, multiple shoots were produced in place of primary branches after reproductive transition, suggesting that a combined action of *AP1/FUL*-like genes and *OsMADS34* are required for IM establishment (Kobayashi *et al.*, 2012). Interestingly, the presence of functional *OsMADS34* in *MADS14;15;18i* triple knockdown plants is sufficient to ensure IM establishment and floret formation (Kobayashi *et al.*, 2012) but when *OsMADS1* is down-regulated in *osmads15* loss-of-function mutants, new plantlets bearing features of a juvenile plant are formed in the panicle. These observations support Goethe's hypothesis that florets in grasses are modified juvenile plantlet meant for reproduction and *OsMADS1* together with *OsMADS15* assures a fertile floret development meant for sexual reproduction (Wang *et al.*, 2010). Additionally, asynergistic interaction between *OsMADS1* and *58* also represses reverse transition from floret-to-spikelet and promotes floret meristen identity (Hu *et al.*, 2015).

OsMADS1 Regulates Floral Meristem Identity and its Maintenance

After establishing the identity to floret meristem, its maintenance is another crucial step for successful completion of reproductive development. This is brought about by maintaining a balance between organogenesis and meristem indeterminacy. In *Arabidopsis*, a complex genetic network involving transcription factors from homeoboxgene family (*WUSCHEL* (*WUS*),*SHOOT MERISTEMLESS* (*STM*), *PHAVOLUTA* (*PHV*), *PHABULOSA* (*PHB*) and *BEL1-like homeodomain* (*BLH*) proteins) and MADS-box gene family(*AGAMOUS*(*AG*), *AGAMOUS-like 24* (*AGL24*), and *SHORT VEGETATIVE PHASE* (*SVP*) controls FM initiation and maintenance (Liu *et al.*, 2009; Rutjens *et al.*, 2009; Ji *et al.*, 2011; Grandi *et al.*, 2012). *ARGONAUTE1* (*AGO1*) and *AGO10* control termination of stem cells in FM by regulating two microRNAs, miR172 and miR165/166, targeting *APETALA2* (*AP2*) and homeo-domain-Zip III (HD-Zip III) members (*PHV* and *PHB*), respectively (Ji *et al.*, 2011). In rice, after securing fertile FM initiation on a spikelet meristem, *OsMADS1* plays key role for the maintenance of FM identity and its eventual termination as a determinate meristem. It activates the expression of four HD-Zip III genes of the REVOLUTA (REV)/RBV clade (*OsHB1–OsHB4*) in rice, of which *OsHB4* is directly regulated by *OsMADS1* (Khanday *et al.*, 2013). Furthermore, it also regulates expression of other homeobox *BLH* genes and a member of YABBY gene family, *TONGARI-BOUSHI1 (TOB1)/OsYABBY5* in developing rice panicles (Khanday *et al.*, 2013). *OsYABBY5* regulates maintenance and determinacy of floret meristem in rice (Tanaka *et al.*, 2012). Thus, all these evidences together suggest that *OsMADS1* may be regulating its FM function by regulating expression of multiple meristem regulators from various families in developing florets.

Arabidopsis AGL24 and *SVP* regulate transition and identity of floral meristem and their expression is directly repressed by *SEP3* (Hartmann *et al.*, 2000; Michaels *et al.*, 2003; Gregis *et al.*, 2008; Kaufmann *et al.*, 2009). Rice genome encodes three *SVP*--like genes, *OsMADS22, 47* and *55* (Lee *et al.*, 2008). Interestingly, they do not regulate flowering time but have conserved functions of regulating meristem identity in rice (Lee *et al.*, 2008). As opposed to the regulation of *AGL24* and *SVP* by *SEP3* in *Arabidopsis*, *OsMADS1* activates expression of two *SVP*-genes, *OsMADS22* and *55* in developing rice panicles,the activation of *OsMADS55* being direct (Khanday *et al.*, 2013), suggesting that despite the conserved functions of rice *SVP*-genes is establishing FM identity, the regulatory relationship between *OsMADS1* and *SVP*-like genes is diverged (Khanday *et al.*, 2013). The positive regulatory relationship between *OsMADS1* and rice *SVP* genes (*OsMADS22* and *55*) are functionally supported as all three genes show overlapping phenotypes upon over-expression during panicle and spikelet development (Prasad *et al.*, 2001; Sentoku *et al.*, 2005; Lee *et al.*, 2008). It is important to note that, *OsMADS55* but not *OsMADS22*, displays flowering time functions in *Arabidopsis* as its over-expression complements early flowering phenotype of *Arabidopsis svp* mutants and causes delayed flowering phenotype in wild-type *Arabidopsis* (Lee *et al.*, 2012). *OsMADS1* also interacts with rice C-class gene, *OsMADS3* and together, they play a role in regulating floret meristem activity maintenance as floret meristem is terminated prematurely in *osmads1-z osmads3-4* double mutants (Hu *et al.*, 2015).

OsMADS1 Functions for Stage-Dependent Activation of Flower Homeotic Genes

In addition to the specification and maintenance of floret meristem, *OsMADS1* also controls identities of floret organs as *OsMADS1* loss-of-function results in development of defective and malformed floret organs (Jeon *et al.*, 2000; Prasad *et al.*, 2005; Agrawal *et al.*, 2005; Chen *et al.*, 2006; Wang *et al.*, 2010; Khanday *et al.*, 2013). Lemma and inner floret organs are homeotically converted to glume-like features with lesser effect on palea in *OsMADS1* down-regulated lines (Prasad *et al.*, 2005). Similar to *Arabidopsis* where SEP factors regulate expression of and interact with ABCD members, *OsMADS1* not only physically interacts (genetically with few of them) with rice ABCD genes (Moon *et al.*, 1999; Lim *et al.*, 2000; Kaufmann *et al.*, 2009; Cui *et al.*, 2010; Hu *et al.*, 2015) but also activates expression of floral homeotic genes including B-Class genes (*OsMADS4* and *16*), C-Class genes (*OsMADS3* &*58*), D-Class genes (*OsMADS13*) and E-Class genes (*OsMADS7* and *8*) (Hu *et al.*, 2015).

Interestingly, activation of rice ABCD genes by *OsMADS1* is not uniform but developmental-stage dependent. A comparison of expression levels of rice homeotic genes between wild-type and *osmads1-z* across various stages of panicle development demonstrates that *OsMADS1* activates expression of meristem function genes such as *OsMADS6, 17, 58* and organ specification genes like *OsMADS7* and *8* at early stage of panicle development whereas activation of *OsMADS4* and *16* (B-Class), *OsMADS3* (C-Class) and *OsMADS13* (D-Class) occurs only at the late stage of development, consistent with their requirement in inner floret organ development and meristem determinacy (Hu *et al.*, 2015). Thus, *OsMADS1* also retains the conserved function of activation of homeotic genes with a slight divergence in rice.

OsMADS1 Plays Diverse Roles in Floral Organ Identity Specification and Organogenesis

SEP genes play redundant but major role in floral organ identity establishment together with ABC class genes in *Arabidopsis* (Pelaz *et al.*, 2000; 2001; Honma and Goto, 2001; Ditta *et al.*, 2004). However, in loss-of-function mutants of rice *OsMADS1* gene alone, floret organs are mis-specified to glume-like identity (Jeon *et al.*, 2000; Prasad *et al.*, 2005; Agrawal *et al.*, 2005; Chen *et al.*, 2006; Wang *et al.*, 2010). Despite general similarity between *Arabidopsis SEP* genes and rice *OsMADS1* for their expression patterns and roles in providing floral organ identities, there exists a partial divergence in their functions. The expression of *Arabidopsis SEP* genes and *OsMADS1* in floral meristem is largely conserved but their expression patterns in the floral organs are diversified. *SEP1* and *2* are expressed in all four floral organs, *SEP3* is restricted to only three inner floral organs and *SEP4* is expressed only in floral center with weak expression in sepals (Flanagan and Ma, 1994; Mandel and Yanofsky, 1998). On the other hand, rice *OsMADS1* is expressed only in lemma/palea (sepal equivalent) and weakly in carpel primordia during floret organogenesis (Prasad *et al.*, 2001).

Corroborated with the distinct expression patterns of *Arabidopsis SEP* genes and rice *OsMADS1*, their regulatory functions and mechanisms are also diverged. While four *SEP* genes are functionally redundant in *Arabidopsis*, rice *OsMADS1* has both, redundant and non-redundant functions during organogenesis. For example, while *OsMADS1* non-redundantly controls lemma-specific differentiation program (Prasad *et al.*, 2001; 2005; Agrawal *et al.*, 2005), it regulates identity of marginal tissues during palea differentiation, redundantly with *OsMADS6* (Ohmori *et al.*, 2009; Li *et al.*, 2010). Though, *OsMADS1* functions cooperatively with *OsMADS15* during FM establishment, their functions are opposite during floret organogenesis. *OsMADS1* controls differentiation of lemma, palea marginal tissues (PMTs), inner floret organs and determinacy. However *OsMADS15* is mainly required for specification of palea and empty glumes (Wang *et al.,* 2010). *OsMADS1* does not express in lodicule and stamens but their development is affected in *osmads1* mutants (Prasad *et al.*, 2001; 2005; Agrawal *et al.*, 2005; Chen *et al.*, 2006). Its early expression in FM or non-cell autonomous signaling may account for its role in specification of lodicules and stamens. Interestingly, functions of *OsMADS1* in specifying lodicule and stamen identity are partially independent of *OsMADS16*-regulated genetic pathway, as evident from the additive phenotypes in *osmads1-z spw1-1* double mutants, on the other hand, a striking similarity between *osmads1* and *osmads7/8* phenotypes suggests that they function in interdependent manner as regards inner three floret organs (Cui *et al.*, 2010; Hu *et al.*, 2015).Furthermore, a genetic analysis of *osmads1-z osmads34* double mutant also demonstrates that both, *OsMADS1* and *OsMADS34,* are required for specifying rice floret organ identity (Gao *et al.*, 2010). Furthermore, *osmads1-z osmads3-4* double mutants show that no inner floret organs are formed, only extra-glume-like structures are developed in the center of the floret, suggesting that a combinatorial action of *OsMADS1* and *OsMADS3* is required for development of inner floret organs (Hu *et al.*, 2015). *OsMADS1* also genetically and physically interacts with *OsMADS6.* Introducing *osmads1* mutation in *osmads6* background enhances its phenotypes (Moon *et al.*, 1999; Ohmori *et al.*, 2009; Li *et al.*, 2010), while over-expression of *OsMADS6* results in formation of additional lodicule-, stamen- and carpel-like organs (Duan *et al.,* 2012). The expression of another *AGL6-like* gene, *OsMADS17* is also directly activated by *OsMADS1*, as demonstrated by the binding of OsMADS1 on a CArG element in *OsMADS17* promoter and the corresponding reduced expression of OsMADS17 in *osmads1-z* florets (Hu *et al.*, 2015).

OsMADS1 Controls Floret Meristem Determinacy through Multiple Genetic Pathways

OsMADS1 is expressed in the floret meristem center and florets of loss-of-function mutants for *OsMADS1* develop multiple abnormal florets with only lemma/palea like structures, mimicking flower-within-flower phenotypes (Jeon *et al.*, 2000; Prasad *et al.*, 2005; Agrawal *et al.*, 2005; Ohmori *et al.*, 2009; Cui *et al.*, 2010; Gao *et al.*, 2010; Li *et al.*, 2010; Wang *et al.*, 2010) and ectopic over-expression of *OsMADS1* leads to premature termination of floret meristem (Prasad *et al.,* 2001). *OsMADS1* modulates/regulates multiple genetic pathways to control meristem determinacy. Homeotic genes of Class-C (*OsMADS3* and *58*) and Class-D (*OsMADS13*) are known to redundantly regulate development of reproductive organs and floret meristem determinacy (Yamaguchi *et al.,* 2006; Dreni *et al.,* 2007; 2011; Li *et al.,* 2011b). Paralogous C-function genes have partially sub-functionalized their functions but they redundantly regulate meristem determinacy (Yamaguchi *et al.*, 2006; Hu *et al.*, 2011; Dreni *et al.*, 2011; 2013). *OsMADS1* activates expression as well as physically interacts with *OsMADS3* and 58 (Hu *et al.*, 2015). Its synergistic interaction with *OsMADS58* controls floret meristem determinacy, evident from phenotypes of *osmads1-z osmads58* double mutants where meristem activity is prolonged in the double mutant (Hu *et al.,* 2015). On the other hand, rice Class-D gene, *OsMADS13* regulates ovule identity and floret meristem determinacy (Lopez-Dee *et al.*, 1999; Dreni *et al.*, 2007, 2011; Li *et al.*, 2011b). The role of *OsMADS1* in controlling floret meristem determinacy is partially independent of *OsMADS13,* as evident from additive phenotypes seen in *osmads1-z osmads13-3* double mutants (Hu *et al.,* 2015).

OsMADS1 and *OsMADS6* redundantly regulate determinacy of floret meristem (Ohmori *et al.*, 2009; Li *et al.*, 2010). The spikelet meristem determinacy is severely impaired in *mfo1-2 lhs1-2* double mutants as compared to single mutants and they develop one or more sequential extra spikelet(s) without inner floret organs (Ohmori *et al.*, 2009). Consistent with their redundant role in controlling meristem determinacy, they regulate expression of a common gene, *OsMGH3/OsGH3-8* encoding an auxin-responsive gene (Prasad *et al.*, 2005; Zhang *et al.*, 2010). Interestingly, down-regulation of *OsMGH3* results in an enlarged carpel growth in a fraction of florets that may be an indication of partial loss of determinacy (Yadav *et al.,* 2011). Interaction of *OsMADS6* with determinacy regulators like *OsMADS3, 58* and *13* also play a role in controlling meristem determinacy.

OsMADS1 Regulates a Balance Between Auxin and Cytokinin Signaling Pathways

Phytohormones, auxin and cytokinin and their interactions with transcription factors are known to regulate floral meristem establishment, organogenesis and meristem determinacy in *Arabidopsis* (Sessions *et al.*, 1997; Benková *et al.*, 2003; Leibfried *et al.*, 2005; Shani *et al.*, 2006; Gordon *et al.*, 2009; Chickarmane *et al.*, 2012; Liu *et al.*, 2014). In addition to controlling leaf polarity and gynoecium patterning, *AUXIN RESPONSE FACTOR 3* (*ARF3*)/*ETTIN* (*ETT*) together with *AGAMOUS* (*AG*) also regulates floral meristem determinacy through repression of the expression of *WUSCHEL* (*WUS*) (Sessions *et al.*, 1997; Chitwood *et al.*, 2009; Liu *et al.*, 2014). Its interaction with *KANADI4* (*KAN4/ATS*) controls ovule development (Kelley *et al.*, 2012). On the other hand, cytokinin induces expression of *WUS* which in turn represses expression of type-A cytokinin response regulators, creating a feedback regulatory loop (Leibfried *et al.*, 2005; Gordon *et al.*, 2009). Importance of cytokinin in regulating FM in rice is evident from the phenotypes of *log* and *ckx2* mutants, functioning in cytokinin biosynthesis and metabolism, respectively (Ashikari *et al.*, 2005; Kurakawa *et al.*, 2007). *OsMADS1* positively regulates auxin signaling pathways at multiple levels and represses overall cytokinin signaling pathways during rice floret development, thus maintaining a critical balance between auxin and cytokinin signaling pathways (Fig. 3; Khanday *et al.*, 2013). *OsMADS1* regulates both upstream (auxin biosynthesis, homeostasis and transport) and downstream (auxin response factors) components of auxin signaling pathways (Khanday *et al.*, 2013). It activates the auxin response by simultaneously promoting the expression of activation domain containing ARFs (e.g. OsARF9, OsARF12, OsARF16, and OsARF25) and repressing expression of the ARFs containing repression domains (e.g. OsARF18) (Khanday *et al.*, 2013). It directly modulates expression of regulators of polar auxin transport (*OsARF-GAP* and *OsPIN1*) and proteolytic degradation-independent ARFs (*OsETTIN2*) (Khanday *et al.*, 2013).

In contrast to auxin signaling pathway, *OsMADS1* represses overall cytokinin signaling pathway during panicle development as the cytokinin levels and/or response was enhanced in *OsMADS1* down-regulated panicles (Khanday *et al.*, 2013). The repression of type-A cytokinin response regulators (e.g. *OsRR1*, *OsRR4* and *OsRR9*) by *OsMADS1* is direct whereas regulation of cytokinin biosynthetic genes (e.g. *LOG*) and type-B response regulators (e.g. *OsRR16* and *OsRR18*) may be indirect (Khanday *et al.*, 2013). Thus, the roles of *OsMADS1* in regulating expression of key transcription factors and controlling a critical balance between auxin and cytokinin signaling pathways indicate that it is a master regulator of key genetic pathways during rice floret meristem transition, establishment, maintenance, organ differentiation and termination of the meristem.

Evolutionary Significance of *OsMADS1* and Future Perspectives

SEP genes are key regulators of reproductive development programs in higher plants (Malcomber and Kellogg, 2005; Litt and Kramer, 2010; Rijpkema *et al.*, 2010). During evolution, grass species have acquired certain novel traits such as higher order branching in inflorescence (i.e. panicle) that provided benefit of producing more seeds. Interestingly, the divergence time-scale of grasses (~60 million years ago) overlaps with the estimated evolutionary divergence of *OsMADS1* sub-clade, indicating that this sub-clade may have co-evolved with grasses in order to acquire grass-specific functions (Doyle, 1973; Prasad *et al.*, 2005; Khanday *et al.*, 2013). This hypothesis is supported by the fact that members of this clade (*OsMADS1*, *5* and *34*) ensure development of grass-specific traits during entire reproductive development in rice (Cui *et al.*, 2010; Gao *et al.*, 2010; Kobayashi *et al.*, 2010). An absence of *OsMADS1* in rice lower florets and its sterility may be correlated, indicating that *OsMADS1* is required to make fertile florets. This is corroborated with the phenotypes of its over-expression in sterile lower florets where it is sufficient to initiate floret-specific developmental programs (Prasad *et al.*, 2001).

In addition to species specific functions of *OsMADS1*, it also interacts with several conserved factors and executes its tissue- and organ-specific regulatory role with them. This could be brought about by forming higher order complexes, the cumulative effects of which define its regulatory functions. Identifying such tissue- and stage-specific higher order complexes would further enhance our understanding on specific roles of *OsMADS1* during development of fertile and determinate florets in rice. Other interesting gap in our understanding is to delineate the role of *OsMADS1* in regulating the differentiation of lodicules and stamens where it is not expressed. It is hypothesized that its early expression throughout floret meristem may have activated lodicule- and stamen-specific developmental programs but the hypothesis is yet to be proved. It would be interesting to specifically silence the expression of *OsMADS1* in the anlagen of lodicule and stamens and study its consequences. Other attractive hypothesis to be investigated is the possible involvement of mobile developmental regulators as seen in other plant tissues. Despite being a master regulator of reproductive development, its upstream regulatory modules have not been thoroughly studied. This is another niche area to be explored in future to enhance the understanding of upstream regulatory modules and get a complete picture of *OsMADS1* mechanistic function in ensuring development of a fertile and determinate rice floret and a successful sexual reproductive trait.

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