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Review

The Roles of MADS-Box Genes from Root Growth to Maturity in *Arabidopsis* and Rice

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Abstract: Rice (*Oryza sativa* L.) and *Arabidopsis thaliana* (L.) life cycles involve several major phase changes, throughout which MADS-box genes have a variety of functions. MADS-box genes are well recognized for their functions in floral induction and development, and some have multiple functions in apparently unrelated developmental stages. For example, in *Arabidopsis*, *AGL15* and *AGL6* play roles in both vegetative development and floral transition. Similarly, in rice, *OsMADS1* is involved in flowering time and seed development, and *OsMADS26* is expressed not only in the roots, but also in the leaves, shoots, panicles, and seeds. The roles of other MADS-box genes responsible for the regulation of specific traits in both rice and *Arabidopsis* are also discussed. Several are key components of gene regulatory networks involved in root development under diverse environmental factors such as drought, heat, and salt stress, and are also involved in the shift from vegetative to flowering growth in response to seasonal changes in environmental conditions. Thus, we argue that MADS-box genes are critical elements of gene regulation that underpin diverse gene expression profiles, each of which is linked to a unique developmental stage that occurs during root development and the shift from vegetative to reproductive growth.

Keywords: MADS-box gene; root growth; floral transition; seed setting; inflorescence branching

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1. Introduction

MADS-box genes are a family of transcription factors initially discovered in eukaryotes [1]. All MADS-box proteins have a DNA-binding MADS domain that is ~60 amino acids in length [2]. There are two types of MADS-domain proteins: Type I and Type II. The functions of Type I proteins in plants are mostly unclear [3]. Type II proteins (also known as MIKC-type proteins) are distinguished by the presence of four different domain structures known as the MADS, keratin-like, intervening, and C-terminal domains [4]. MIKC-type MADS-box genes are known to play roles in plant development from vegetative growth to reproduction and to function in various stress responses [5].

The conserved MADS (M) domain and a substantial variable area at the C-terminus are found in Type I proteins, also known as the M-type [6]. In addition to the MADS DNA binding activity, the M domain contains an I domain, a K domain, and a C domain in Type II proteins [7]. The I domain is required for DNA dimerization and specificity [8], whereas the K domain is required for both dimer formation and tetramerization [9,10]. The C domain, a highly variable and largely unstructured domain based on secondary structure prediction, is important in transcriptional activation and the development of higher-order transcription factor (TF) complexes. The C domain also contributes to MADS-box protein–protein interactions [10,11]. Based on the ABCDE model, M-type MADS-box genes have been reported to be involved in plant reproduction, specifically the development and functioning of female gametophytes, the embryo, and the endosperm; MIKC-type

MADS-box genes are involved in meristem differentiation, flowering, the determination of floral organ identity, and fruit development [11].

Genetic studies in rice and *Arabidopsis* have revealed the functions of several MADS-box genes in plant development. The majority of these studies have shown that MADS-box genes are engaged in a variety of important morphological and physiological functions, including gametophyte cell division, root development, the floral transition, and floral organ control [12–14]. A typical dicot flower is divided into four parts (whorls): petals, sepals, pistils, and stamens. The generally accepted ABCDE model of floral organs is based on research in dicot species such as *Antirrhinum majus* and *Arabidopsis* [15,16]. Different floral organ identities are regulated by various gene combinations, namely A + E (sepals), A + B + E (petals), B + C + E (stamens), C + E (carpels), and D + E (ovules). A great majority of these genes encode MADS-box TF that have been linked to floral organ development [17–21].

In *Arabidopsis* and rice, MADS-box genes play roles in a variety of developmental processes, including root development and elongation, meristem specification, the flowering transition from vegetative to reproductive stage, endosperm and seed formation, flower development and fertility, and fruit ripening. Several published reviews have reported on their functions from vegetative transition to reproductive development [1,11,22–28].

2. MADS-Box Gene Expression Profiles during Root Development

MADS-box genes are involved in various components of root development [29], affecting the formation of primary and lateral roots, root density, and root elongation. More than 50 MADS-box genes have been reported to be expressed in *Arabidopsis* roots [30]. However, little is known about their role in root growth and development during environmental stress exposure. In *Arabidopsis*, many MADS-box genes of the MIKC type, specifically *AGL17*-like clade genes, regulate root formation [31,32]. Three members of the *AGL17*-like clade, namely *AGL17*, *AGL21*, and *ANR1*, are dominantly expressed in *Arabidopsis* roots [30,33–35]. Expression of the nitrate transporter gene *NRT2.1* is reduced in the roots of an *anr1* mutant line, demonstrating that *ANR1* is a positive regulator of *NRT2.1* in *Arabidopsis* [36]. *ANR1* stimulates lateral root elongation and increases the fresh weight of shoots in the presence of nitrate by promoting lateral meristem activity [33,37]. In contrast, *AtAGL21* increases auxin biosynthesis in the absence of nitrate, promoting lateral root development and elongation [33,37,38]. Intriguingly, *ANR1* expression was drastically reduced in *nrt1.1* mutants, and these mutants displayed reduced root elongation in nitrate-rich conditions compared with *ANR1*-knockout plants [33,39]. These findings demonstrate that *NRT1.1* functions upstream of *ANR1* in local nitrate-induced lateral root development. The key roles of *ANR1* in shoot development and in response to nitrate stress remain to be investigated. Overexpression of miR444a decreases shoot development at the seedling stage [40]. Future research should also focus on miR444a and *ANR1* may work cooperatively or independently to understand the function of *ANR1* under nitrate stress exposure in processes such as shoot development at the seedling stage. The MADS-box TF *AGL16* functions as a negative regulator under saline conditions. The *agl16* mutants are salt stress-resistant concerning root elongation in comparison to wild-type plants [41]. In *Arabidopsis*, *AGL42* expression has been utilized as a marker for quiescent center identity cells [42], which are the cells at the apices of stele and cortex histogens. However, the loss-of-function mutant has no clear abnormal phenotype in the root, demonstrating that its role in root elongation is unknown. Furthermore, it has been shown that upregulation of *AGL42* in the quiescent center and the stele depends on expression of the Brassinosteroid receptor *BRI1* on epidermal cells [43].

In rice, *AGL17-like* clade genes such as *OsMADS57* regulate root growth and elongation [29,44,45]. *OsMADS57* promotes seminal and adventitious root elongation as well as root to shoot nitrate translocation by influencing the expression of *NRT2* [46,47], whereas overexpression of *OsMADS57* in rice increases the rate of seed germination and root elongation in response to salt stress conditions [48]. It remains to be determined whether

OsMADS57 overexpression promotes tolerance to other environmental stress factors such as drought or heat. Additional research should be conducted to understand the OsMADS57-mediated stress signaling pathway to ultimately strengthen crop tolerance to adverse environmental factors through genome editing technology.

OsMADS50/OsSOC1 (*Oryza Sativa SUPPRESSOR OF OVEREXPRESSION OF CO 1*) was shown to be important in the control of crown root growth [49]. Plants overexpressing *ANR1* showed increased lateral root density and longer lateral roots under control conditions and high nitrogen levels [37]. Furthermore, the rice *ANR1* gene family members *OsMADS27*, *OsMADS25*, and *OsMADS61* are expressed in the root vasculature, and their transcription is modulated differentially in response to NO_3^- deficiency, NO_3^- resupplementation, and a variety of environmental conditions [35,44]. In the presence of nitrate, *OsMADS25*-overexpression lines showed increases in the number and density of lateral roots while producing significantly larger primary roots; knocking down *OsMADS25* had the opposite effect on transgenic rice plants. In addition, *OsMADS25* is involved in the regulation of nitrogen transporter genes, demonstrating that this TF is a key regulator of primary and lateral root formation in rice [29]. In the absence of NO_3^-, overexpression of *OsMADS25* resulted in increased lateral root number and primary root length in *Arabidopsis* compared with wild-type plants. *OsMADS27*-overexpression lines of rice produced more lateral roots but had shorter primary roots in a NO_3^- dependent manner. Surprisingly, *OsMADS27* overexpression improved salt tolerance, most likely via changes in ABA signaling [50]. Similarly, phosphate deficit and phosphorus supplementation decreased the expression of *OsMADS23*, *OsMADS25*, and *OsMADS27*, but sulphur deficiency increased the expression of these genes significantly [35]. In a yeast two-hybrid experiment, *OsMADS27* was shown to bind to a protein implicated in ABA signaling (*ABI5*; [50]). *OsMDP1* encodes a rice AG-like MADS-box protein found in vegetative tissues such as the coleoptile, mature leaf, culm internode, root-elongation zone, and most significantly, the joining area between the leaf blade and the sheath [51]. These findings indicate that several MADS-box genes are critical in root development in many species, and that they respond to environmental conditions through complicated regulatory mechanisms.

Expression of the *XAANTAL1* (*XAL1*; formerly known as *AGL12*) ortholog *OsMADS26* increases with age in rice, and overexpression of this MADS-box gene produces a variety of stress-related responses, including decreased root growth and development [52]. Furthermore, another *XAL1* ortholog, *LOC_Os08g02070*, is expressed preferentially in the rhizome tips in another rice species, *Oryza longistaminata* [53]. Analysis of the root transcriptome in wild emmer wheat (*Triticum turgidum* ssp. *dicoccoides* (Körn.) Thell.) showed that the *OsMADS26* ortholog *MADS26* was upregulated in a drought-resistant genotype compared to a drought-susceptible line, implying that *XAL1* homologs contribute to varying degrees to stress responses and plant development [54]. *XAL1* is expressed during the development of various organs, suggesting that it is a key component in complex networks that affect multiple aspects of plant development. Furthermore, it is likely to be implicated in both vegetative and reproductive epidermal cell patterning under different environmental circumstances. However, additional research is required to test this hypothesis. Future research should also focus on protein–protein interactions to understand the function of *XAL1* in processes such as root growth.

3. MADS-Box Gene Expression Profiles during Leaf Development in Rice

It has been shown that *OsMADS22* and *OsMADS55* encode negative regulators of brassinosteroid responses, although their functions differ significantly by developmental stage. *OsMADS47* is expressed at high levels in seedling leaves, whereas the transcription of *OsMADS55* is highest in mature leaves. As a result of these contrasting expression patterns, *OsMADS55* and *OsMADS47* are the primary negative regulators of brassinosteroid responses in leaves [55]. In the lamina joint of flag leaves in *osmads22 osmads47 osmads55* triple mutant plants, two genes downstream of brassinosteroid synthesis (*OsXTR1* and *OsBLE3*) were upregulated, whereas expression of two brassinosteroid biosynthesis

genes (*DWARF2* and *BRD1*) did not significantly change. These findings suggest that genes in the short vegetative phase group interfere with the downstream signaling of *OsXTR1* and *OsBLE3*. Further studies into the interactions between proteins encoded by brassinosteroid-responsive genes and downstream target genes are needed to verify this hypothesis. Transgenic plants with reduced levels of *OsMADS55* or *OsMADS47* expression show brassinosteroid-related aberrant phenotypes [51].

Gibberellic acid (GA) plays an important role in the regulation of seed germination, leaf shape, and flowering. The gibberellic acid response element, the P-box, is present in the promoter region of *PvSOC1*, but not in the promoters of *SOC1/AGL20* or *OsSOC1*. The expression of *PvSOC1*, from the bamboo *Phyllostachys violascens*, was found to be higher in the leaves of seedlings after GA treatment, indicating a positive response to GA. *PvSOC1* appears to be a multifunctional gene that influences leaf development and flowering [56]. *PvSOC1* over-expression in *Arabidopsis* and rice resulted in early flowering, abnormal floral organs, and deformed leaves. However, further research is required to identify the function of *PvSOC1* in rice and *Arabidopsis*.

4. MADS-Box Genes Are Responsible for Inflorescence Branching

The molecular processes driving the evolutionary and developmental dynamics of inflorescences are largely unknown. This is in contrast to the relatively well-understood genetic foundation of floral diversity, where MADS-box TFs have been revealed to play a key role in reproductive processes [57,58]. Grasses (Poaceae), which include cereal crops such as rice, have a different inflorescence design than eudicots such as *Arabidopsis*. Spikelets, which are physically separate structural components, make up the inflorescence in grasses. In *Arabidopsis*, it has been reported that both *APETALA1* (*AP1*; formerly known as *AGL7*) and *LEAFY* (*LFY*) inhibit inflorescence branching through interaction with the *TERMINAL FLOWER1* (*TFL1*) gene [59–61]. Furthermore, two *AP1* homologs, *CAULIFLOWER* (*CAL*) and *FRUITFULL* (*FUL*; formerly known as *AGL8*) repress the expression of *TFL1*. This was verified in *ap1 cal ful* triple mutants, in which *TFL1* functions in conversion of floral meristems into inflorescences [62]. Four MADS-box TFs, *SOC1*, *SVP*, *AGL24*, and *SEPALLATA 4* (*SEP4*), suppress inflorescence branching by directly inhibiting *TFL1* expression in *Arabidopsis* [63]. It was further demonstrated that *SVP*, *SOC1*, *AGL24*, and *SEP4* orthologs in rice control panicle branching by modulating *TFL1*-like genes. These findings demonstrate the existence of a conserved genetic mechanism in flowering plants that determines inflorescence morphology. Studies of the gene expression programs downstream from *LFY* and *AP1* have shown that *LFY* and *AP1* share several target genes and frequently bind to contiguous locations in the *Arabidopsis* genome [59,64–67]. The findings of a meta-analysis of existing genome-wide data sets for the two TFs confirmed a common set of target genes [66]. *LFY* and *AP1* regulate the expression of ~200 genes, many of which are known regulators of floral development and branching. These common targets most likely form the molecular foundation of the partial redundancy observed between *AP1*/*CAL* and *LFY* in floral development. However, it is still unknown whether *LFY* and *AP1*/*CAL* work independently or cooperatively in regulating the common target genes. MADS-box genes reported participating in different developmental processes of *Arabidopsis* are tabulated in Table 1.

TFL1 has an apparently conserved function; mutant rice plants ectopically expressing *TFL1* orthologs exhibit massive inflorescence branching [63,68]. It is therefore unknown how *TFL1*-like genes are expressed in flowering plants to define specific types of inflorescence design. In eudicots and monocots, *TFL1*-like genes are needed for meristem indeterminacy [68–71]. Upregulation of the *TFL1* homologs *RCN1* and *RCN2* in rice and *ZCN1* to *ZCN6* in maize results in a branched inflorescence [68,70]. Future research should examine the relationships between these MADS-box genes and other inflorescence characteristics. For example, a study of *OsMADS34*, *FLORAL ORGAN NUMBER4* (*FON4*), and *LAX PANICLE1* (*LAX1*) showed superior phenotypes of *osmads34 fon4* and *osmads34 lax1* double mutants compared with the single mutants; *OsMADS34* interacts with *LAX1* and

FON4 to regulate many features of inflorescence shape, branching, and meristem activity. Furthermore, a double mutant combining the sterile lemma-defective and *osmads34* mutants had longer and wider sterile lemmas, indicating that *ELONGATED EMPTY GLUME* (*ELE*) and *OsMADS34* work together to control sterile lemma development. *OsMADS34* and *OsMADS15* may also cooperate to control the development of sterile lemmas [72].

Table 1. Roles of MADS-box genes in the development of *Arabidopsis thaliana* (L.).

Gene	Locus ID	Function	Reference
STK/AGL11	At4g09960	Ovule development	[19,30]
XAL1/AGL12	At1g71692	Root development; transition to flowering	[73]
AGL15	AT5g13790	Embryogenesis; sepal and petal longevity; flowering repressor with *AGL18*; fruit maturation	[74–76]
AGL18	At3g57390	Flowering repressor with *AGL15*	[77]
AGL16	At3g57230	Number and distribution of stomata	[78]
AGL17	At2g22630	Root formation; Flowering activator	[31,32,79]
AGL6	At2g45650	Flowering activator; lateral organ development	[80]
FLC/AGL25	At5g10140	Juvenile-to-adult transition; flowering repressor; flowering initiation, flower organ development	[81,82]
MAF2/AGL31	At5g65050	Flowering repressor	[83]
AGL19	At4g22950	Flowering activator	[84]
FUL/AGL8	At5g60910	Meristem identity specification; annual life cycle regulator with *SOC1*; fruit development	[62,85]
AP1/AGL7	At1g69120	Homeotic A-class gene; meristem identity specification	[62]
AGL24	At4g24540	Flowering activator	[86]
AGL23	At1g65360	Embryo sac development	[87]
AGL28	At1g01530	Flowering activator	[88]
AGL42	At5g62165	A marker for quiescent center identity cells	[42]
AGL62	At5g60440	Central cell development	[89]

5. Communicating Role from Vegetative to Flowering Transition

One of the most basic developmental alterations in the life cycle of flowering plant species is the change from the vegetative to the reproductive stage [90]. Several investigations have shown that flower growth in higher eudicot angiosperms is controlled by a hierarchical network of regulatory genes [91]. Late- and early-flowering genes, which are regulated by diverse environmental factors such as light quality, day length, and heat, are at the top of the hierarchy. These genes may regulate the conversion from vegetative to flowering development by activating meristem identity genes in response to environmental factors.

In *Arabidopsis*, SPLs are upstream activators and downstream targets of the floral-transition MADS-box genes. Photoperiod strongly affects transcription of three miR156-targeted SPLs (*SPL3*, *SPL4*, and *SPL5)*, which are downregulated in short-day (SD) conditions and upregulated in long-day (LD) conditions [92]. Another study demonstrated that *SPL3*, *SPL4*, and *SPL5* act in a dependent manner upon two related BELL1-like homeodomain proteins, PENNYWISE (PNY) and POUND-FOOLISH (PNF), which act to specify floral meristems through downregulation of miR156 [93]. This effect was verified in *pny pnf* double mutants, in which expression levels of *AP1* and three SPLs were drastically reduced and plants were not able to produce flowers in response to inductive conditions. Further research is needed to determine whether miR156 regulation of flowering is dependent on the expression of *PNY* and *PNF*. *SPL3* is regulated directly by *SOC1* [94]; *SPL4* expression is

greatly decreased in *soc1 ful* double mutants in the SAM [94,95]. This interconnected feed-forward loop may promote the transition from vegetative to reproductive development. The reduction in miR156 accumulation in *agl15 agl18* double mutants demonstrates that *AGL15* and *AGL18* function as co-regulators with miR156 in the determination of flowering time in *Arabidopsis*. *AGL15* and *AGL18* interact with putative CArG motifs in the MIR156 promoter both in vitro and in vivo [96–98].

In *Arabidopsis*, GA enhances the transition from vegetative to flowering development by degrading transcriptional repressors DELLAs. However, the underlying processes are still unknown. DELLA proteins interact with microRNA156-targeted SPL TFs to repress transcriptional activation of MADS-box genes such as *AP1*, *SOC1*, and *FUL*, plant-specific *LEAFY* (*LFY*) TFs, and miR172 [99–102].

In rice, the MADS protein family has 75 members, which are mainly divided into five categories: MIKCC, MIKC, Mα, Mβ, and Mγ. Most are involved in regulating the formation of floral organs [103] but MADS-box TFs are also related to several processes in vegetative plant growth and development. There have been no reports of rice genes with substantial similarity to *FLOWERING LOCUS C* (*FLC*; formerly known as *AGL25*) outside of the MADS genes; however, the MADS-box gene *OsMADS50*/*OsSOC1* has a similar sequence to that of *AtSOC1*. It has been shown that *OsMADS50*/*OsSOC1* is transcribed at a somewhat higher level during the floral transition than during vegetative growth, and that *OsMADS50*/*OsSOC1* over-expression causes transgenic *Arabidopsis* plants to flower early [104].

OsMADS50 and *OsMADS56* encode MIKCC-type proteins that are homologs of *Arabidopsis SOC1*, and the expression of both is affected by the circadian clock [105,106]. Under LD conditions, *OsMADS50* and *OsMADS56* have opposing effects on flowering time in rice. *OsMADS56* is a flowering suppressor gene, whereas *OsMADS50* can promote flowering. In *Arabidopsis*, *SOC1* is a downstream target gene of *CONSTANS* (*CO*), whereas *OsMADS50* and *OsMADS56* are upstream of the flowering time regulatory network in rice. In addition, expression analyses and interaction experiments for related genes have shown that they also control flowering in rice by forming an antagonistic complex to regulate the common downstream gene *OsLFL1-Ehd1* (*Early heading date 1*). They are also independent of flowering regulation by *Hd1*, *SE5*, and *RID1*/*OsId1*/*Ehd2* [107].

Rice flowering time is determined by the expression levels of three additional *SEP*-like MADS-box genes, *OsMADS7*, *OsMADS5*, and *OsMADS8* [108,109]. *TaMADS1*, a wheat homolog of rice *OsMADS24*, regulates floral development, and ectopic expression of *TaMADS1* induces early flowering in *Arabidopsis* [5]. Overexpression of *TaMADS1* also induces early flowering and abnormal floral organ development in *Arabidopsis* [110]. Furthermore, *TaAGL6* overexpression also promotes early flowering in *Arabidopsis* [111]. Several studies have shown that specific MADS-box genes in wheat affect flowering; however, compared to species such as *Arabidopsis* and rice, there is still a great deal to be uncovered.

OsMADS14, *OsMADS15*, and *OsMADS18* are all *AP1*/*FUL* genes that encode flowering promoting factors that function downstream of *OsMADS50* [105,112]. RNAi-mediated suppression of these three genes results in a slight delay in the reproductive transition [112]. *OsMADS51* and *OsMADS65* are MADS-box genes of the MIKCC type, and *OsMADS51* encodes a TF that promotes flowering under SD conditions [113].

6. Molecular Events at the Shoot Apical Meristem in Response to Photoperiodic Induction

Arabidopsis Florigen gene *FLOWERING LOCUS T* (*FT*) transcription and migration of the encoded protein to the apical meristem are induced by inductive photoperiods, which alter the regulation of genes involved in inflorescence formation. The FT–FD complex in *Arabidopsis* shoot apical meristems is directed to the promoter of *AP1*, which encodes a MADS-box TF required for flowering initiation and flower development [114]. Additional MADS-box TFs that are necessary for *FT*-stimulated flowering, such as *SOC1*, is upregulated early in the floral conversion. In *Arabidopsis*, *SOC1* is regulated by two flowering regulators, *CO* and *FLC*, which function as a floral activator and repressor, respectively [100,115,116].

Other genes, such as *FD PARALOGUE* (*FDP*), may share *FD* function [114,117]. *TWIN SISTER OF FT* (*TSF*) and *FD* activation by N^6-benzylaminopurine treatments and physical interaction between TSF and FD or FDP proteins [118] demonstrated that a TSF/FD(P) complex is involved in promoting flowering [119]. Expression levels of both *TSF* and *FDP* increased simultaneously in the leaves after N^6-benzylaminopurine application, suggesting that the *TSF*/*FD* complex may function in leaves. This was a surprising finding because FD is primarily expressed in *Arabidopsis* root and shoots apices [114,117]. However, it has also been reported that *FD* is necessary for *FT* to increase gene expression in leaves [120], and the *FD* homolog *SPGB* (an AG-box factor called SPGB with a specific 14-3-3 adapter protein) is expressed in both leaves and shoot apices in tomato [121]. The discovery of the TSF protein in phloem sap [122] demonstrates that it could be a systemic signal. This indicates that N^6-benzylaminopurine initiates flowering by promoting transcription of *TSF*, which then travels to the meristem and stimulates *SOC1* and *AP1* transcription by contact with FD or FDP. Prior to the floral transition, flowering repressors are also present in the meristem. *FLC* and *SVP* encode MADS-box proteins that significantly delay flowering [99,123–125]. These proteins form a heterodimer that is hypothesized to suppress *SOC1* transcription [126,127]. However, a study revealed that the flowering time was increased in *flc svp* double mutants compared with either single mutant, implying that these proteins have both unique and overlapping functions. Both proteins delay flowering by suppressing *FT* and *TSF* or *SOC1* transcription in the leaf and meristem, respectively [118,128,129]. The MADS-box floral activator *FUL* functions redundantly with *SOC1*, as demonstrated by the phenotypes of *soc1* and *ful* single mutants [62,85,95]. The *soc1 ful* double mutants had increased abnormalities in floral initiation and reproductive growth maintenance.

Both *Hd3a* and *OsFD1* expression are necessary in rice protoplasts to stimulate the expression of *OsMADS15*, a homolog of *AP1*. The *hd3a* mutants that cannot bind to 14-3-3 proteins and *14-3-3* knockouts are unable to stimulate *OsMADS15* transcription [130]. Rice has a counterpart to *SOC1* that is regulated by *OsMADS50* and has been found to be necessary for flowering induction [105]. The MADS-box genes *OsMADS14*, *OsMADS18*, and *OsMADS34* are required for normal inflorescence development, and their expression is elevated in the SAM during the flowering transition [112]. These findings point to the presence of a conserved floral initiation strategy in plant apical meristems, in which florigens interact with FD-like TFs to induce transcription of several MADS-box genes slightly earlier in the transition from vegetative growth to flowering. This core developmental plan is linked to additional regulatory layers in order to fine-tune and sustain the floral transition [131,132]. Figure 1 includes several MADS-box genes responsible for root, seedling, flowering, ovule, and pollen grain development of *Arabidopsis*.

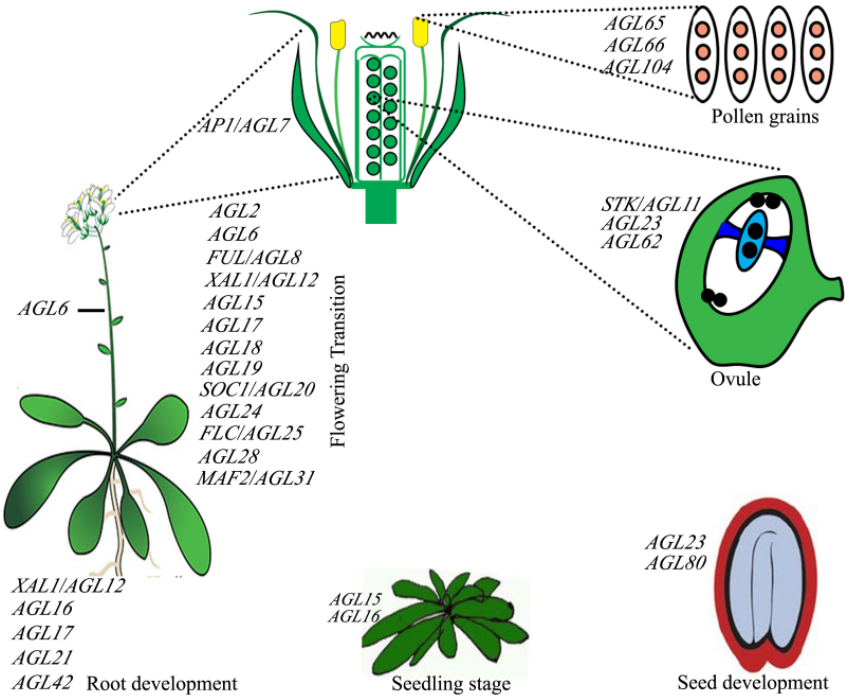

Figure 1. The biological roles of MADS-box genes in controlling the development of various vegetative and reproductive tissues of the model plant *Arabidopsis thaliana*. Many MADS-box genes mediate the transition to flowering. Some MADS-box genes are involved in flowering time, such as *AGL2* [133,134], *AGL6* [80], *FUL/AGL8* [62,85], *XAL1/AGL12* [73], *AGL15* [74–76], *AGL17* [79], *AGL18* [77], *AGL19* [84], *SOC1/AGL20* [100], *AGL24* [135], *FLC/AGL25* [81,82], *AGL28* [88], and *MAF2/AGL31* [83]. MADS-box genes are also involved in root growth (e.g., *XAL1/AGL12*, *AGL16*, *AGL17*, *AGL21*, and *AGL42*) [31,32,42,73,78,79,136], pollen maturation and tube growth (*AGL65/66/104*) [137], ovule development (e.g., *STK/AGL11*, *AGL23*, *AGL62*) [19,30,87,89], and seed development (e.g., *AGL23*, *AGL80*) [87,138].

7. Floret Pattern Initiation and Development

Although key aspects related to the genesis and diversity of flowers remain largely unknown, the genetic control of flower shape has been widely investigated in diverse crop species [139].

MADS-box proteins regulate inflorescence development by establishing a higher-order combination, and rice has a large number of MADS-box genes [140]. The four putative A-class genes in rice are *OsMADS14*, *OsMADS18*, *OsMADS15*, and *OsMADS20* [140,141]. The double knockouts *osmads14 osmads15* exhibit genuine homozygous genetic variation, with abnormalities in the first and second whorls. The A-class gene *OsMADS15* has been demonstrated to be involved in palea development in a previous study [142]. Triple mutant *osmads14 osmads15 osmads18* plants show no phenotypic changes in floral development [112]. Rice also has two B-class orthologs, *OsMADS2* and *OsMADS4*. It was demonstrated that *osmads4* mutant plants have normal lodicule and stamen characteristics, whereas transgenic plants in which *OsMADS2* silenced show differences in the lodicules but not in the stamens. Instead of lodicules and carpel-like organs, transgenic plants lacking both *OsMADS4* and *OsMADS2* have palea-like structures [143–146]. The C-class gene *OsMADS3* is associated with meristem function in early and late floral development [147], whereas the D-class gene *OsMADS13* is required for ovule identity [148]. *OsMADS3* is mainly involved in the presumptive region of stamen and ovule primordia just before the initiation of these organs [148]. Furthermore, *OsMADS58* is upregulated in reproductive organs. However, loss-of-function mutants for *OsMADS3* have abnormal stamens but normal carpel development. The *osmads58* mutant has decreased floral meristem determinacy instead of floral organ abnormalities. When *OsMADS3* and *OsMADS58* were silenced, the

male and female reproductive organs were homeotically transformed into palea/lemma-like organs and lodicules [148]. It is possible that differences in the proteins that interact with *OsMADS3* and *OsMADS58* resulted in functional diversity. The precise molecular mechanism behind the functional diversification of *OsMADS3* and *OsMADS58* remains an interesting subject for future study. Overexpression of SVP-group MADS-box genes produces flower deformities and floral reversion in *Arabidopsis* and barley [135,149], and Sentoku et al. [150] showed that *OsMADS22*-overexpressing plants exhibit comparable traits. Fertility and panicle length were also affected in *OsMADS22*-overexpressing plants. Similarly, *OsMADS55* overexpression lines showed reduced fertility, shorter panicles, and malformed flowers [55].

OsMADS1, a *SEP*-like subfamily homolog, is expressed in the lemma and palea and affects floral meristem identity [151]. The interaction of *OsMADS1* with B-, C-, and D-class proteins has been confirmed by yeast two-hybrid analysis; this interaction produces a heterodimeric complex that influences floral meristem determinacy. The interaction of *OsMADS1* with *OsMADS3* and *OsMADS58* to determine stamen identity and prevent spikelet meristem reversion has been demonstrated both in vitro and in vivo. Furthermore, *OsMADS1* is a positive regulator of *OsMADS17* during floral development, whereas *OsMADS1* and *OsMADS13* function in meristem determinacy through partially independent pathways. These findings suggest that *OsMADS1* collaborates with another unknown regulator to modulate meristem determinacy. *OsMADS1* and *OsMADS34* are involved in the development of the four whorls of the floral organs as well as the development of spikelet meristems [152]. This finding has been verified in *osmads34 osmads1* double mutants, demonstrating that *OsMADS34* determines rice floral organ identity in combination with *OsMADS1*.

The S-clade genes *OsMADS62* and *OsMADS63*, as well as the P-clade gene *OsMADS68*, are MIKC-type genes in rice. All three MIKC-type genes were found to be expressed in the late developmental stages of pollen. Proteins from the different sub-clades form heterodimers, which is very similar to the process that occurs in *Arabidopsis* [153,154]. *OsMADS62*, *OsMADS63*, and *OsMADS68* transcripts are found in pollen but not in the anther walls. These findings show that rice MIKC-type genes are only expressed in pollen at late developmental stages, implying that they participate in pollen maturation [153]. The *osmads62 osmads63 osmads68* triple knockout mutants have a male-sterile phenotype [155], similar to that of the *rice immature pollen 1 (rip1*) mutant. *RIP1* functions in normal pollen development, and *rip1* mutants have a male-sterile phenotype and abnormal intine layers [156]. Furthermore, *RIP1* is not expressed in *osmads62 osmads63 osmads68* triple mutants. It has been predicted that *RIP1* may function upstream of *OsMADS62, OsMADS63*, and *OsMADS68,* or in a different pathway containing those three *MADS* genes. Further study is required to verify this prediction. MADS-box genes reported participating in different developmental processes of rice are tabulated in Table 2.

In *Arabidopsis*, several genes play critical roles in floret development. *TM5*, *FBP2*, and other *AGL2*-like genes are expressed in the petals and stamens [133,157,158]. In addition, the *AGL2*-like genes serve as facilitators between the floral organ identity and floral meristem genes in *Arabidopsis* [133,134]. *SEEDSTICK* (*STK*; formerly known as *AGL11*), *SHATTERPROOF (SHP) 1*, and *SHP2* are three D-class genes in *Arabidopsis* that have overlapping functions in regulating ovule development [19,159,160]. This redundancy has been verified through phenotyping single and triple mutants. *XAL1/AGL12*, the sole member of the subfamily in *Arabidopsis*, is expressed in flowers [34].

Table 2. MADS-box genes have different functions in different parts of the rice plant.

Gene	Genomic Identity	Function	Reference
OsMADS1	LOC_Os03g11614	Involved in the early stages of rice floret development	[161]
OsMADS3	LOC_Os01g10504	Meristem function in early and late floral development, involved in the formation of stamens and ovules	[147]
OsMADS5	LOC_Os06g06750	Expressed strongly across a broad range of reproductive stages and tissues	[162]
OsMADS7	LOC_Os08g41950	Improves the stability of rice amylose content at high temperature	[163]
OsMADS8	LOC_Os09g32948	Inflorescence branch meristems	[152]
OsMADS13	LOC_Os12g10540	Ovule identity	[148]
OsMADS14	LOC_Os03g54160	Flowering activator	[112]
OsMADS15	LOC_Os07g01820	Flowering activator	[112]
OsMADS16	LOC_Os06g49840	Regulation of floral organ development and pollen formation	[164]
OsMADS17	LOC_Os04g49150	Regulates hormone signaling and floral identity	[103]
OsMADS18	LOC_Os07g41370	Flowering activator	[112]
OsMADS25	LOC_Os04g23910	*OsMADS25* overexpression results in more lateral roots	[29]
OsMADS26	LOC_Os08g02070	Expressed in rice leaves and inflorescences	[165]
OsMADS27	LOC_Os02g36924	Produced more lateral roots	[50]
OsMADS29	LOC_Os02g07430	Involved in programmed cell death (PCD) in the developing embryonic cell nuclear region	[166,167]
OsMADS34	LOC_Os03g54170	Involved in development of the inflorescence	[152]
OsMADS50	LOC_Os03g03100	Flowering activator	[107]
OsMADS51	LOC_Os01g69850	Flowering activator	[113]
OsMADS56	LOC_Os10g39130	Flowering suppressor	[107]
OsMADS57	LOC_Os02g49840	Expressed in root vasculature	[35,44]
OsMADS61	LOC_Os04g38770	Expressed in root vasculature	[35,44]
OsMADS62	LOC_Os08g38590	Rice anther development	[168]
OsMADS63	LOC_Os06g11970	Rice anther development	[168]
OsMADS68	LOC_Os11g43740	Pollen development	[153]
OsMADS77	LOC_Os09g02780	Endosperm development	[169]
OsMADS87	LOC_Os03g38610	Endosperm development	[170]
OsMADS89	LOC_Os01g18440	Endosperm development	[170]

8. MADS-Box Genes Play an Important Role in Seed Setting and Development

There are several key reproductive phases in the life cycle of an angiosperm that lead to sufficient seed setting. Pollination and subsequent fertilization of the ovules in the flower are key events to produce viable seeds. A large number of MADS-box mutants in flowering plant species implies that members of this gene family perform important regulatory functions in diverse conditions during seed development [34,171]. *AGL21* inhibits seed germination in *Arabidopsis* under osmotic stress conditions in addition to its function in lateral root development [172]. Seeds of *AGL21* loss-of-function lines germinate at a lower rate than wild-type plants under salt stress (150 mM NaCl), severe osmotic stress (300 mM mannitol), and ABA treatment. *AGL21* controls the activity of *ABI5*, which is required for ABA signaling, and *ABI5* is required for *AGL21*-regulated seed germination. *AGL15* is involved in seed formation, and overexpression lines show delayed silique maturity and seed desiccation [14].

In the rice genome, the MADS-box genes are members of a large TF family containing almost 75 members [103]. The majority have reported involvement in floral organ development, and some are important for endosperm development [63,173]. For example, *OsMADS29* is involved in seed development [166,167,174]; *OsMADS87* is involved in endosperm cellularization and seed size regulation [175]. Heat treatment (from moderate to severe) for 48 h after fertilization reduces the expression of three rice MADS-box genes, *OsMADS82*, *OsMADS87*, and *OsMADS89*, leading to reduced size and viability of rice seeds [175]. This observation led researchers to investigate *OsMADS87* in mutant rice lines [175]. They discovered that RNAi lines maintained under ideal conditions showed increased endosperm cellularization (the process during which the endosperm exits the multi-nucleate stage and initiates cytokinesis) and decreased grain size due to reduced *OsMADS87* expression. However, *OsMADS87* overexpression was found to have no effect on endosperm cellularization but resulted in larger mature seeds. When heat-stressed plants (35 °C) were compared to control plants, the overexpression and wild-type lines had smaller seeds, but the RNAi lines were unaffected. It has also been reported that *OsMADS87* expression is temperature sensitive and negatively associated with increased expression of *OsFIE1*, the only PRC2 complex member with heat sensitivity in ripening rice seeds [176]. The *Arabidopsis* homolog *PHE1* is responsible for early endosperm development, although its role in seed size development is unknown. Moreover, rice plants with both stable amylose concentration at high temperatures and spikelet fertility can be obtained by inhibiting *OsMADS7* function during endosperm development [163]. These findings suggest that *OsMADS7* is a promising candidate gene for maintaining stable amylose contents in rice at high temperatures. Specifically reducing the expression of *OsMADS7* during rice endosperm formation may be an effective strategy for breeding high-quality rice that is tolerant of temperature stress.

Several key genes are expressed in *Arabidopsis* during seed development. *AGL62* controls the timing of endosperm cellularization; this process occurs prematurely in loss-of-function of *agl62* mutants, limiting normal embryo development [89]. *AGL23* has been linked to the formation of both female gametophytes and seeds. After megasporogenesis, *agl23* mutant ovules are partially inhibited, implying that *AGL23* plays a function in early embryo sac development [87]. *AGL28* is a unique type I MADS-box gene because, in addition to the embryo sac development, it is expressed in a variety of organs during seed development [88].

It is worth mentioning that B-sister genes, a novel collection of MIKC MADS-box genes, are close relatives of B-type genes [31]. B-sister proteins are found in both gymnosperm and angiosperm species [166,177–179]. B-sister genes are important for ovule and seed establishment in *Arabidopsis* [31,180,181]. An *Arabidopsis* B-sister gene, *ARABIDOPSIS BSISTER* (*ABS*), controls endothelial growth and proanthocyanidin (PA) accumulation in the seed coat [181–183]. *GORDITA* (*GOA*), another *Arabidopsis* B-sister gene, regulates ovule coat production and fruit longitudinal development in a novel and non-redundant manner [184].

The MADS-domain TF STK is involved in ovule identity determination [183] and transmission tract development [185,186], and also plays a pivotal role in seed abscission [187,188]. The *stk* mutants are reported to have smaller seeds compared with wild-type plants [19]. *STK* increases cell cycle progression in seeds via *E2Fa*, a pathway that is considered critical for seed size regulation [189]. It has also been reported that STK is necessary for endothelium differentiation in conjunction with *ABS* [181]. In *Arabidopsis thaliana*, mutations in *XYLOSIDASE1* (*XYL1*) have a significant impact on seed germination, seed size, and fruit development. The MADS-box TF *STK* regulates *XYL1* expression, which is directly involved in developing seeds and fruit [190]. Figure 2 includes several MADS-box genes responsible for root, seedling, flowering, ovule, and pollen grain development of rice.

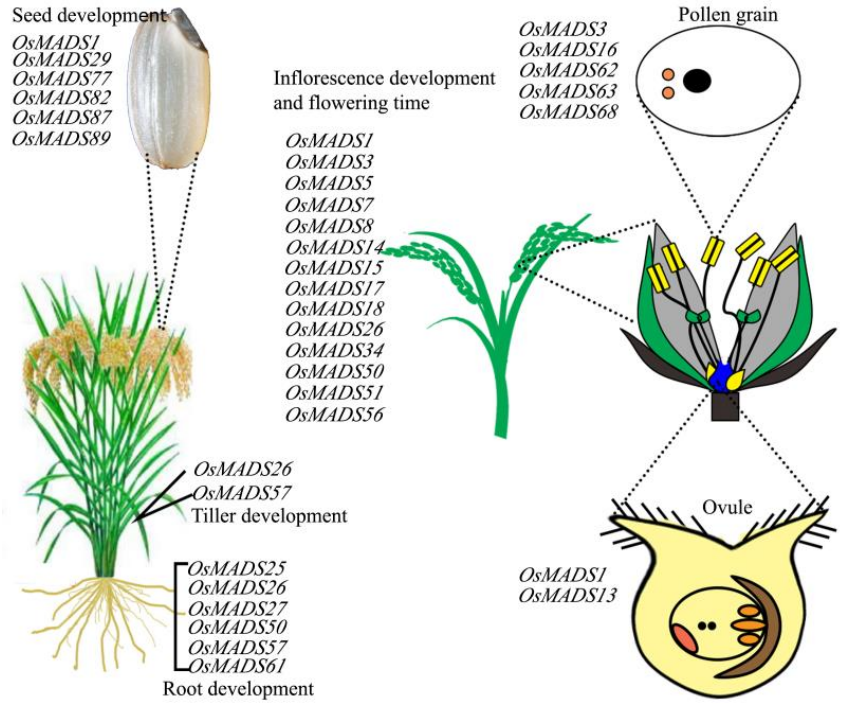

Figure 2. The biological roles of MADS-box genes in controlling the development of various vegetative and reproductive structures in the rice plant. Many MADS-box genes mediate the transition to flowering induction (e.g., *OsMADS1* [161], *OsMADS3* [147], *OsMADS5* [162], *OsMADS7* [163], *OsMADS8* [152], *OsMADS14* [112], *OsMADS15* [112], *OsMADS17* [103], *OsMADS18* [112], *OsMADS26* [165], *OsMADS34* [152], *OsMADS50* [107], *OsMADS51* [113], and *OsMADS56* [107]). MADS-box genes involved in tiller development include *OsMADS26* [191] and *OsMADS57* [50]. Those involved in root development include *OsMADS25* [44], *OsMADS26* [191], *OsMADS27* [50], *OsMADS50* [49], *OsMADS57*, and *OsMADS61* [38,44]; in ovule growth, *OsMADS1* [161] and *OsMADS13* [148]; in pollen grain maturation, *OsMADS3* [147], *OsMADS16* [164], *OsMADS62*, *OsMADS63* [168], and *OsMADS68* [153]; and in seed and endosperm development, *OsMADS1* [161], *OsMADS29* [166,167,174], *OsMADS77* [169], *OsMADS82* [175], *OsMADS87* [170,175], and *OsMADS89* [170,175].

9. Concluding Remarks and Future Perspectives

Alterations in gene regulation are one of the most significant routes leading to phenotypic changes. Due to their capacity to affect gene expression, TFs can cause developmental shifts. TFs have also been shown to function in regulating responses to environmental stress throughout the plant life cycle. Furthermore, small changes in the expression of a few key TFs have been shown to impact the development of numerous processes and structures. Specific mutants have shown that TFs from the MADS-box gene family are important regulators of *Arabidopsis* development at all growth stages. Multiple studies have also shown that MADS-box genes play important roles in controlling plant responses and tolerance to a wide variety of abiotic stimuli, highlighting their relevance as integrators of environmental signals and endogenous hormones in a taxonomically diverse range of plant species.

Several functional investigations have been undertaken into the developmental roles of MADS-box genes in rice; however, a great deal remains unknown. Gene knockdown mutants (single and higher-order) should be identified to expose the functional characteristics of MADS-box genes throughout the development of rice plants. In addition, the interactions of MADS-domain proteins with other proteins will aid in determining the molecular functions of MADS-box genes in rice. The functional diversification process of duplicated MADS-box genes, including *OsMADS2*, *OsMADS3*, *OsMADS4*, and *OsMADS58*, should

also be addressed. Such an investigation, along with analogous observations in other grass species, will contribute to the understanding of how grass flowers and inflorescences evolved and diversified.

The significance of MADS-box genes has mainly been investigated in the model plant *Arabidopsis thaliana*. The literature reviewed here, however, demonstrates that our understanding is quickly evolving with respect to MADS-box genes that govern flower development in rice due to the novel functional genomics methods now possible. The rapid advances in this area were primarily a result of knowledge gained in *Arabidopsis* [192]. Many mutant populations based on transposons and T-DNA insertions are accessible for functional investigations of rice genes [193,194]. CRISPR-Cas9 systems have been widely exploited today as tools for genome editing in a variety of plant species [195,196]. A technique that uses chemical mutagens such as ethyl methanesulfonate (EMS) can also be used to study gene function via reverse genetics [197–199].

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