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*Review*

# Thinking out of the box: MADS-box genes and maize spikelet development

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**Due to the importance of maize as an agricultural crop and its stature as an ideal model plant for the study of developmental biology in monocots, it is natural that research into its genetic structure has gained worldwide attention. Unfortunately, although much progress has been made in our understanding of the genetic control of the maize spikelet over the last decade, the depth of research in this field still lags behind that of dicots. Here, we review the developmental features of the maize spikelet and the characterization and function of MADS-box genes with the hope of stimulating further research in this area.**

**Key words:** Maize spikelet, ABC model, MADS-box genes, regulation.

## INTRODUCTION

Among the multitude of developmental phases in plants, flower formation is the most exciting and complex one. About 20 years ago, the ABC model for the genetic control of flower development was proposed and was initially based on the analysis of floral homeotic mutants in *Arabidopsis thaliana* and *Antirrhinum majus*. Later, the genetic regulatory network of flowering and floral meristem also began to be elucidated upon. Among these genes, transcription factors, especially MADS-box genes, play crucial roles in the whole regulation network (Krizek and Fletcher, 2005). Poaceae (grasses) is one of the most species-rich flowering plant families and includes many economically important crops. Flowers of grasses are arranged in spikelets, in which glumes, lemma, palea and lodicules are characteristic organs and serve as a basis for the classification of grasses (Schmidt and Ambrose, 1998). However, it still remains controversial whether they are equivalent to the bract, sepal and petal of dicot flowers. Thus, more research on the development of grass spikelets will provide a further understanding of the genetic control of monocot flower development and the molecular evolution of the grass-specific floral organs.

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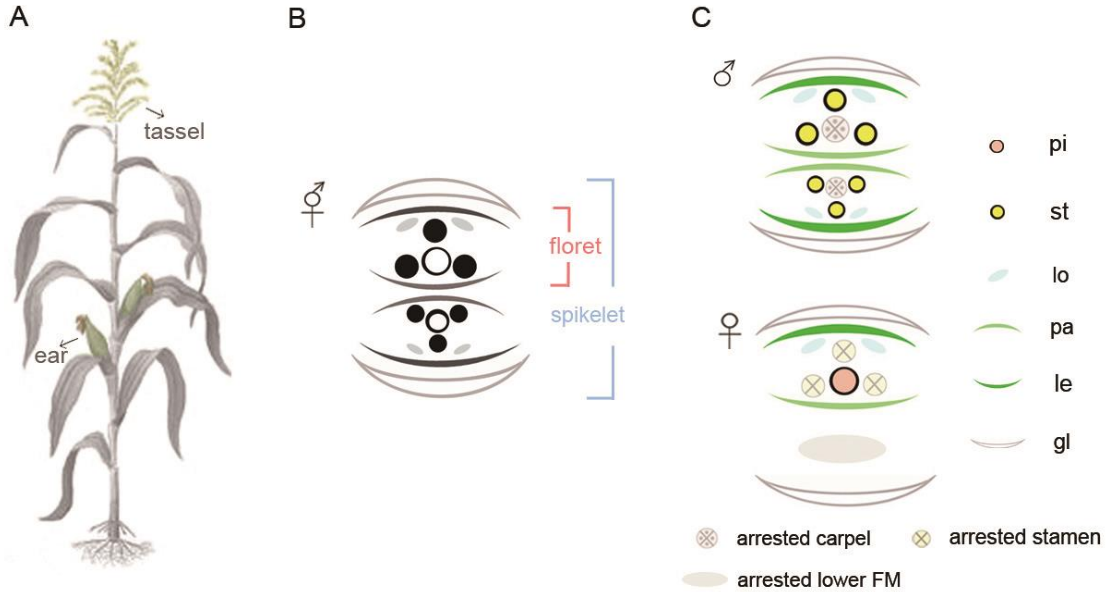

**Figure 1.** Maize plant and floral development. (A) Mature maize plant. **(B)** Maize floral development. At an early developmental stage, the spikelet is bisexual. **(C)** Mature spikelet. Later in development, pistils arrest in the floret of male spikelet (up) and the stamens arrest in the floret of female spikelet (below). **Pi,** pistil; **st,** stamen; **lo,** lodicules; **pa** palea, **le** lemma; **gl,** glume.

As one of the most important agricultural crops in the world, maize (*Zea mays* L. ssp. mays) is an important model plant for grass developmental biology because it possesses all of the following: a rich genetic history and abundant developmental mutants, a fully sequenced genome, and a good synteny with other grass species. Additionally, unlike rice producing hermaphrodite flowers, maize is a monoecious plant. Thus, research on the development of maize spikelets will contribute largely to understanding monocot plant flower development, the regulation mechanism of sex determination, and molecular evolution of the grass-specific floral organs. In this review, we summarize recent findings concerning maize spikelet development, mainly focusing on the characterization and functional study of MADS-box genes in maize flower organ development.

## THE DEVELOPMENTAL STRUCTURE OF MAIZE SPIKELET

Maize is a monoecious plant that forms male and female inflorescence on a terminal tassel and on lateral ears, respectively (Figure 1A). At an early developmental stage, tassel and ear both initiate bisexual spikelets. Each spikelet contains two florets, the upper and the lower floret, which are subtended by two glumes. Each floret consists of a lemma, a palea, two lodicules, three stamens and a pistil (Figure 1B). Later in development, pistils cease to develop in the floret of male spikelets, and two unisexual florets form as a result of the pistil abortion; while in female spikelets, the lower floret and the stamens in the upper floret abort, resulting in each ear spikelet bearing a single female floret (Figure 1C). Therefore, unisexual flowers in maize are achieved by the process of selective arrest and abortion of the pistil or stamen primordium within a bisexual floret at the appropriate time (Thompson et al., 2009).

## THE CHARACTERISTICS OF MADS-BOX GENES

MADS-box genes encode a family of transcription factors that play crucial roles in higher eukaryotes, especially in the regulation of floral development in flowering plants (Ciaffi et al., 2011). Previous phylogeny reconstructions revealed that the MADS-box gene family is composed of several defined gene clades. Almost all the plant MADS-box genes that are currently known are members of a monophyletic superclade of genes with a conserved structural organization, including a MADS (M-), intervening (I-), keratin-like (K-) and C-terminal (C-) domain, so called MIKC-type domain structure (Münster et al., 2002) (Figure 2). Some conserved motifs in the C-terminal domain play an important role in the formation of the MADS-box protein complex and transcription activation (Theissen et al., 1996). Many MIKC-type MADS-box genes that regulate floral development have been identified in angiosperms and can be divided into 12 major subfamilies by phylogeny reconstructions, including *AG, AGL6, AGL12, AP3*/*PI*, *GGM13* ($B_s$), *STMADS11*, *TM3*, *AGL2*, *AGL17*, *AP1*/*SQUA*, *AGL15* and *FLC*

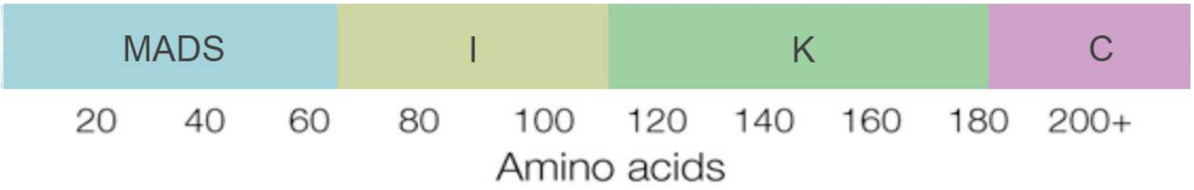

**Figure 2**. Domain structure of plant MIKC-type MADS-box protein.

(Becker and Theissen, 2003). So far, at least 32 MADS-box genes, belonging to 9 subfamilies, have been reported from maize and are widely involved in the regulation of floral organ identity, determinacy of the floral meristem, flowering time and the development of seeds (Table 1) (Zhao et al., 2011). Some maize MADS-box genes are functionally conservative with their orthologous genes in dicot plants, while the functions of others still await verification.

## MAIZE HOMEOTIC MADS-BOX GENES

Studies on the two model eudicot plants *Arabidopsis* and *Antirrhinum* have led to the classic genetic ABC model that explains how three classes of genes (A, B and C) work together to specify floral organ identity. This model holds that A-class genes specify sepal fate in the first flower whorl, A plus B genes specify petals in the second whorl, B plus C genes give rise to stamens, and C genes alone are needed for carpel development in the fourth whorl (Coen and Meyerowitz, 1991). Later, the model has been expanded to incorporate D class genes, which are responsible for the development of ovules (Angenent et al., 1995), and E-class genes, which are necessary for the normal expression of A, B , C and D class genes and for the formation of functional complexes (Pelaz et al., 2000; Ditta et al., 2004). D class genes specify ovules, which will develop into seeds after pollination. Thus, some scholars define the model as “ABCDE model” (Goto et al., 2001). With the exception of the A-class gene *AP2*, all of those genes are members of the MIKC-type MADS-box family of transcription factors and they act by forming dimers and complexes of higher order. In *Arabidopsis*, there are two different class A genes, *APETALA1* (*AP1*) and *APETALA2* (*AP2*), two class B genes, *APETALA3* (*AP3*) and *PISTILLATA* (*PI*), one class C gene, *AGAMOUS* (*AG*) (Theissen et al., 2000), and one class D gene, *SEEDSTIK* (*STK*). The class E genes in *Arabidopsis* are represented by *SEP*-like genes (also known as AGL2 subfamily), namely *SEPALLATA1, 2, 3, 4* (*SEP1, 2, 3, 4*) (Ditta et al., 2004). Mutations of these genes will result in homeotic conversions of the regulated floral organs into organs of adjacent floral whorls, so these genes are also called homeotic genes. At present, the candidate class A, B, C, D and E genes from maize have been obtained by cDNA cloning, but it is still unclear whether the function of these genes is fully conservative with the homologous genes of dicotyledonous plants (Münster et al., 2002). Despite this, some important indications have been gained from the comparative functional analysis of rice orthologs (Cui et al., 2010; Kobayashi et al., 2010; Wang et al., 2010).

### Putative A-class genes in maize

By cDNA isolation and phylogenetic sequence analysis, Münster et al. (2002) have found an orthologous relationship among *ZAP1* in maize, *AP1* in *Arabidopsis* and *OsMADS15* in rice. *OsMADS15* has been confirmed to control the differentiation of lemma and palea (Wang et al., 2010), two floral organs positionally orthologous to sepals, whereas until now only northern blot analysis gives us a limited clue of *ZAP1* as a putative A class gene that *ZAP1* was expressed in lemma, palea and lodicules, but not in anthers and carpel, similar with the expression pattern of *AP1* in *Arabidopsis* (Münster et al., 2002). Additionally, two other MADS-box genes, *ZMM4* and *ZMM15,* are orthologous genes of *AP1* and *OsMADS14* (Itoh et al., 2005). Because of the lack of the corresponding mutants, more supporting data is required before it can be determined whether or not these mentioned maize MADS-box genes have strict class A functions.

### Putative B-class genes in maize

Compared to class A genes, the functions of class B genes have been proved to be conservative between monocots and eudicots. *Silky1* (*Si1*) in maize is an orthologous gene of *AP3* in *Arabidopsis*. *Si1* was expressed in anthers and lodicules. Compared to wild-type plants, *si1* mutants showed homeotic conversion of stamens to carpels and lodicules to palea/lemma-like structures, which suggest that palea/lemma in maize are homologous organs to sepals and lodicules are homologous to petals (Ambrose et al., 2000). Additionally, there are at least three class B genes in maize, *ZMM16*, *ZMM18* and *ZMM29*, which are orthologous genes of *PI* in *Arabidopsis* (Whipple et al., 2004). Whipple et al. (2004) have demonstrated that ZMM16 is capable of interacting *in vitro* with Si1, as well as with the orthologous

**Table 1.** MIKC-type MADS-box genes in maize.

| Subfamily | Gene | Expression domain | Putative function | References |
|---|---|---|---|---|
| *AG* | *ZAG1* | Carpel, anther | *AG* orthologous gene | Schmidt et al., 1993 |
| | *ZAG2* | Mature carpel | *STK* orthologous gene | Schmidt et al.,1993; Theissen et al., 1995 |
| | *ZMM1* | — | *STK* orthologous gene | Theissen, 1995 |
| | *ZMM2* | Anther | *AG* orthologous gene | Theissen, 1995 |
| | *ZMM23* | — | *AG* orthologous gene | Münster et al., 2002 |
| | *ZMM25* | — | *STK* orthologous gene | Münster et al., 2002 |
| *AGL2* | *ZMM3* | — | *SEP-like* gene | Kobayashi et al., 2010 |
| | *ZMM6* | Developing kernels and vegetative tissues | *SEP-like* gene | Lid et al., 2004; Kobayashi et al., 2010 |
| | *ZMM7* | — | *SEP-like* gene | Fischer et al., 1995 |
| | *ZMM8* | Upper floret meristem | *SEP-like* gene | Cacharrón et al., 1999; Kobayashi et al., 2010 |
| | *ZMM14* | Upper floret meristem | *SEP-like* gene | Cacharrón et al., 1999; Kobayashi et al., 2010 |
| | *ZMM24* | Spikelet meristem | *SEP-like* gene | Kobayashi et al., 2010 |
| | *ZMM27* | Developing kernels and vegetative tissues | *SEP-like* gene | Lid et al., 2004; Kobayashi et al., 2010 |
| | *ZMM31* | Spikelet meristem | *SEP-like* gene | Kobayashi et al., 2010 |
| *AGL6* | *ZAG3* | Floral meristem, palea, lodicule, carpel | meristem gene | Becker and Theissen, 2003; Thompson et al., 2009 |
| | *ZAG5* | Carpel | — | Becker and Theissen, 2003; Thompson et al., 2009 |
| *AGL17* | *ZmMADS2* | Anther, pollen tube | Anther dehiscence | Schreiber et al., 2004 |
| *PI (DEF/ GLO)* | *SILKY1* | Anther, lodicule primordium | *AP3* orthologous gene | Ambrose et al., 2000 |
| | *ZMM16* | — | *PI* orthologous gene | Whipple et al., 2004 |
| | *ZMM18* | — | *PI* orthologous gene | Whipple et al., 2004 |
| | *ZMM29* | — | *PI* orthologous gene | Whipple et al., 2004 |
| *SQUA* | *ZAP1* | Lemma, palea, lodicule | *AP1* orthologous gene | Münster et al., 2002 |
| | *ZMM4* | Leaf primordia, young inflorescence | Early flowering | Danilevskaya et al., 2008 |
| | *ZMM15* | — | — | Danilevskaya et al., 2008 |
| | *ZMM28* | — | — | Münster et al., 2002 |
| | *ZmMADS3* | Stem node, egg cell | Meristem gene, fertility | Heuer et al., 2001 |
| *STMADS11* | *ZMM19* | — | *Tunicate1* | Han et al., 2012; Wingen et al., 2012 |
| | *ZMM20* | — | — | Münster et al., 2002 |
| | *ZMM21* | — | — | Münster et al., 2002 |
| | *ZMM26* | — | — | Münster et al., 2002 |
| *TM3* | *ZmMADS1* | Egg cell, central and antipodal cells | — | Heuer et al., 2001 |
| *Bs* | *ZMM17* | Inflorescence, ovule | Reprodutive organs evolution | Becker et al., 2002 |

*AP3*. They have also shown that maize B-class genes are capable of rescuing the corresponding *Arabidopsis* B-class mutants, providing additional evidence of class B conservation *(*Whipple et al., 2004). Though there is still lack of studies on maize *PI*-genes related mutants, several lines of evidence from rice give us clues about their possible functions. Using RNAi and yeast two-hybrid strategy, *OsMADS2*, rice orthologous gene of *ZMM16*, has been proved to play an important role in lodicule and stamen development; in contrast, *OsMADS4*, orthologue of *ZMM18* and *ZMM29*, mainly takes part in stamen development (Prasad and Vijayraghavan, 2003; Yoshida et al., 2007; Yao et al., 2008). Thus, at least to some extent, we can make an easy speculation that, as putative

class B gene, duplicated *PI* clade MADS-box genes may function redundantly in maize stamen and lodicule development.

## Putative C-class genes in maize

The typical class C gene of *Arabidopsis AG* is involved in controlling of floral determinacy and specification of carpel and stamen identity (Yanofsky et al., 1990; Coen and Meyerowitz, 1991). Such C gene activity may be diversified in maize because of gene duplication event. Maize contains two subclades of putative C-lineage genes, *ZAG1* and *ZMM2/ZMM23* (Kramer et al., 2004; Zahn et al., 2006; Dreni et al., 2007). The speculation about maize C function diversification is supported by the observations from their rice orthologous genes. A knockout line of *OsMADS3* (orthologous to *ZMM2/ZMM23*) and *OsMADS58* (orthologous to *ZAG1*) showed that both gene function as C-class genes. However, *OsMADS3* had a stronger role in specifying stamen identity and *OsMADS58* was more relevant in conferring floral meristem determinacy and in regulating carpel morphogenesis (Yamaguchi et al., 2006). Similarly, in the maize *zag1* mutants, floral meristem determinacy was partially lost, whereas stamens were almost normal in male flowers, suggesting that other class C genes, such as *ZMM2* and *ZMM23*, may be responsible for stamen specification. The expression pattern of *ZAG1* and *ZMM2* was consistent with this hypothesis; *ZAG1* is mainly expressed in carpels, while *ZMM2* is mainly expressed in anthers (Schmidt et al., 1993; Theissen et al., 1995; Mena et al., 1996). On the basis of these indications, *ZAG1* probably specifies floral meristem determinacy and *ZMM2/ZMM23* may specify organ identity of stamens, though mutants of *ZMM2/ZMM23* have not yet been identified.

## Putative D-class genes in maize

Arabidopsis contains only one D class gene *STK*, which is involved in ovule development and seed dispersal (Pinyopich et al., 2003). By contrast, maize has three duplicated D class genes: *ZMM1* and *ZAG2*, together with rice *OsMADS13*, *Brachypodium BdMADS2* and wheat *TaAG-3*, belongs to one subclade, and *ZMM25* lies in another subclade with *OsMADS13*, *BdMADS2* and T*aAG-4*, according to phylogenetic analysis of D-lineage gene among grasses (Pinyopich et al., 2003; Paolacci et al., 2007; Ciaffi et al., 2011; Wei et al., 2013). Similar to *STK* gene, *ZAG2* primarily expressed in carple and ovule (Schmidt et al., 1993; Lopez-Dee et al., 1999). However, till now no more information have been gained about maize D class genes. Fortunately, recent studies on their grass counterparts may provide some interesting clues. Besides, expressing with a similar pattern with *ZAG2*, the *osmads13* knock-out mutant was completely female sterile, and its ovules were converted into a reiteration of ectopic carpels or into more amorphous structures with carpel identity (Dreni et al., 2007). Interestingly, knock-out of *osmads21* had a normal phenotype; moreover, *osmads21* could not modify the *osmads13* phenotype (Dreni et al., 2007). These data suggest that *OsMADS13* plays a role in ovule identity determination and floral meristem determinacy, while *OsMADS21* has probably lost this function during evolution (Dreni et al., 2007). In line with this, expression pattern and functional divergence have also been revealed among D lineage genes in wheat and *Brachypodium* (Paolacci et al., 2007; Wei et al., 2013). More or less, such divergence may also lie in the putative maize D class genes.

## Putative E-class genes in maize

In *Arabidopsis*, class E genes function as cofactors with class A, B, and C genes, and in the absence of all four SEP genes, floral organs are transformed into leaf-like structures (Pelaz et al., 2000; Ditta et al., 2004). At least eight class E genes have been identified in maize and five in rice (Zahn et al., 2005; Arora et al., 2007; Cui et al., 2010; Ciaffi et al., 2011). Sequence analysis showed that *ZMM8* and *ZMM14* are orthologous to *OsMADS1* (*LHS1*) in rice (Cacharrón et al., 1999). *ZMM3* is orthologous to *OsMADS5*, *ZMM6* is orthologous to *OsMADS7*, *ZMM27* is orthologous to *OsMADS8*, and *ZMM24* and *ZMM31* are orthologous to *OsMADS34* (*PAP2*) (Kobayashi et al., 2010). *ZMM8* and *ZMM14* are found expressed in the all floral organs of the mature upper floret, but not in the lower floret. Cacharrón claimed that *ZMM8* and *ZMM14* work as selector genes to distinguish the upper from the lower floret during spikelet development (Cacharrón et al., 1999). In other words, *ZMM8* and *ZMM14* may be involved in conferring the identity or determinacy of the upper floret meristem, or they may prevent the conversion of the floret meristem into a spikelet meristem. *In situ* hybridization experiments revealed that *ZMM6* and *ZMM27* are not expressed during the vegetative growth period of maize, weakly expressed in the development of inflorescence, and strongly expressed during maize kernel development. But neither single mutant nor the *zmm6 zmm27* double mutant displays any obvious abnormities in kernel or flower development, suggesting that other SEP-like genes may provide functional redundancy with *ZMM6* and *ZMM27* (Lid et al., 2004) .

Rice has five SEP-like genes, *OsMADS1*, *OsMADS5*, *OsMADS57, OsMADS8* and *PAP2*/*OsMADS34*, whose functions are similar to SEP-like genes in *Arabidopsis* (Agrawal et al., 2005; Prasad et al., 2005; Cui et al., 2010; Kobayashi et al., 2010). However, it is still unclear whether the precise function of SEP-like genes in maize is conservative to the orthologous genes in *Arabidopsis* or rice (Malcomber and Kellogg, 2004). Some research shows that the SEP-like genes in grass have a complex genetic lineage and a variety of expression patterns. These findings indicate that the SEP-like genes in grass are likely to undertake more function than their orthologous genes in *Arabidopsis* (Malcomber and Kellogg, 2004). However, it is still unclear whether the precise function of SEP-like genes in maize is conservative to the orthologous genes in *Arabidopsis* or rice (Malcomber and Kellogg, 2004). Some research shows that the SEP-like genes in grass have a complex genetic lineage and a variety of expression patterns. These findings indicate that the SEP-like genes in grass likely have additional functions to their orthologous genes in *Arabidopsis* (Malcomber and Kellogg, 2004).

## PROSPECTS

Because of the agricultural and biological importance of maize, research on the roles of MADS-box genes in maize spikelet development has attracted worldwide attention. Although, research indicating that MADS-box genes regulate maize spikelet development has made great progress, it is still in the early stages. Many maize MADS-box genes were obtained by homologous cloning, but their expression patterns and function still remain unclear. The accumulating data from studies on MADS-box genes in dicots provide a guideline for the research of MADS-box genes in maize spikelet development. However, because of the unique floral structure of maize, whether or not the research of MADS-box genes in *Arabidopsis* can be applied to maize and other important crops needs to be verified by more powerful and diverse technologies. These could include isolation of maize mutants in related to MADS-box related genes, expression profiling of MADS-box genes, and the comparative study of their regulatory networks, and implementation of the maize Floral Genome Project (FGP). All of these studies will help to explore the function of MADS-box genes in maize and broaden our understanding of the molecular development and evolution of maize and other grass spikelets. Acquiring more understanding of MADS-box genes in maize spikelet development will promote awareness of the floral developmental mechanism of maize and other monocot plants.

### Conflict of Interest

The author(s) have not declared any conflict of interests.

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## REFERENCES

Agrawal GK, Abe K, Yamazaki M, Miyao A, Hirochika H (2005). Conservation of the E-function for floral organ identity in rice reveal by the analysis of tissue culture-induced loss-of-function mutants of the *OsMADS1* gene. Plant Mol. Biol. 59(1):125-135.

Ambrose BA, Lerner DR, Ciceri P, Padilla CM, Yanofsky MF, Schmidt RJ (2000). Molecular and genetic analyses of the *silky1* gene reveal conservation in floral organ specification between eudicots and monocots. Mol. Cell. 5(3):569-579.

Angenent GC, Franken J, Busscher M, van Dijken A, van Went JL, Dons HJ, van Tunen AJ (1995). A novel class of MADS-box genes is involved in ovule development in petunia. Plant Cell 7(10):1569-1582.

Arora R, Agarwal P, Ray S, Singh AK, Singh VP, Tyagi AK, Kapoor S (2007). MADS-box gene family in rice: genome-wide identification, organization and expression profiling during reproductive development and stress. BMC Genomics 8:242.

Becker A, Kaufmann K, Freialdenhoven A, Vincent C, Li MA, Saedler H, Theissen G (2002). A novel MADS-box gene subfamily with a sister-group relationship to class B floral homeotic genes. Mol. Genet Genomics 266(6):942-950.

Becker A, Theissen G (2003). The major clades of MADS-box genes and their role in the development and evolution of flowering plants. Mol. Phylogenet. Evol. 29(3): 464-489.

Cacharrón NJ, Saedler H, Theissen G (1999). Expression of MADS box genes *ZMM8* and *ZMM14* during inflorescence development of *Zea mays* discriminates between the upper and the lower floret of each spikelet. Dev. Genes Evol. 209(7):411-420.

Ciaffi M, Paolacci AR, Tanzarella OA, Porceddu E (2011). Molecular aspects of flower development in grasses. Sex Plant Reprod. 24(4):247-282.

Coen ES, Meyerowitz EM (1991). The war of the whorls: genetic interactions controlling flower development. Nature 353(6339): 31-37.

Cui R, Han J, Zhao S, Su K, Wu F, Du X, Xu Q, Chong K, Theissen G, Meng Z (2010). Functional conservation and diversification of class E floral homeotic genes in rice (*Oryza sativa*). Plant J. 61(5): 767-781.

Danilevskaya ON, Meng X, Selinger DA, Deschamps S, Hermon P, Vansant G, Gupta R, Ananiev EV, Muszynski MG (2008). Involvement of the MADS-box gene *ZMM4* in floral induction and inflorescence development in maize. Plant Physiol. 147(4):2054-2069.

Ditta G, Pinyopich A, Robles P, Pelaz S, Yanofsky MF (2004). The *SEP4* gene of *Arabidopsis thaliana* functions in floral organ and meristem identity. Curr. Biol. 14(21): 1935-1940.

Dreni L, Jacchia S, Fornara F, Fornari M, Ouwerkerk PB, An G, Colombo L, Kater MM (2007). The D-lineage MADS-box gene *OsMADS13* controls ovule identity in rice. Plant J. 52(4): 690-699.

Fischer A, Baum N, Saedler H, Theissen G (1995). Chromosomal mapping of the MADS-box multigene family in *Zea mays* reveals dispersed distribution of allelic genes as well as transposed copies. Nucleic Acids Res. 23(11): 1901-1911.

Goto K, Kyozuka J, Bowman JL (2001). Turning floral organs into leaves, leaves into floral organs. Curr. Opin. Genet. Dev. 11(4):449-456.

Han JJ, Jackson D, Martienssen R (2012). Pod Corn Is caused by rearrangement at the *Tunicate1* Locus. Plant Cell. 24(7):2733-2744.

Heuer S, Hansen S, Bantin J, Brettschneider R, Kranz E, Lorz H, Dresselhaus T (2001). The maize MADS-box gene *ZmMADS3* affects node number and spikelet development and is co-expressed with *ZmMADS1* during flower development, in egg cells, and early embryogenesis. Plant Physiol. 127(1):33-45.

Itoh JI, Nonomura KI, Ikeda K, Yamaki S, Inukai Y, Yamagishi H, Kitano H, Nagato Y (2005). Rice plant development: from zygote to spikelet. Plant Cell Physiol. 46(1):23-47.

Kobayashi K, Maekawa M, Miyao A, Hirochika H, Kyozuka J (2010). *PANICLE PHYTOMER2* (*PAP2*), encoding a SEPALLATA subfamily MADS-box protein, positively controls spikelet meristem identity in rice. Plant Cell Physiol. 51(1):47-57.

Kramer EM, Jaramillo MA, Di Stilio (2004). Patterns of gene duplication and functional evolution during the diversification of the *AGAMOUS* subfamily of MADS-box genes in angiosperms. Genetics 166(2): 1011-1023.

Krizek BA, Fletcher JC (2005). Molecular mechanisms of flower development: an armchair guide. Nat. Rev. Genet. 6(9):688-698.

Lid SE, Meeley RB, Min Z, Nichols S, Olsen OA (2004). Knock-out mutants of two members of the AGL2 subfamily of MADS-box genes expressed during maize kernel development. Plant Sci. 167(3):575-582.

Lopez-Dee ZP, Wittich P, Enrico Pè M, Rigola D, Del Buono I, Gorla MS, Kater MM, Colombo L (1999). *OsMADS13*, a novel rice MADS-box gene expressed during ovule development. Dev. Genet. 25(3): 237-244.

Malcomber ST, Kellogg EA (2004). Heterogeneous expression patterns and separate roles of the *SEPALLATA* gene *LEAFY HULL STERILE1* in grasses. Plant Cell. 16(7):1692-1706.

Mena M, Ambrose BA, Meeley RB, Briggs SP, Yanofsky MF, Schmidt RJ (1996). Diversification of C-function activity in maize flower development. Science 274(5292): 1537-1540.

Münster T, Deleu W, Wingen LU, Cacharrón NJ, Ouzunova M, Faigl W, Werth S, Kim JT, Saedler H, GT (2002). Maize MADS-box genes galore. Maydica 47(3-4):287-301.

Paolacci AR, Tanzarella OA, Porceddu E, Varotto S, Ciaffi M (2007). Molecular and phylogenetic analysis of MADS-box genes of MIKC type and chromosome location of *SEP*-like genes in wheat (*Triticum aestivum* L.). Mol. Genet. Genomics 278(6): 689-708.

Pelaz S, Ditta GS, Baumann E, Wisman E, Yanofsky MF (2000). B and C floral organ identity functions require *SEPALLATA* MADS-box genes. Nature 405(6783):200-203.

Pinyopich A, Ditta GS, Savidge B, Liljegren SJ, Baumann E, Wisman E, Yanofsky MF (2003). Assessing the redundancy of MADS-box genes during carpel and ovule development. Nature 424(6944): 85-88.

Prasad K, Parameswaran S, Vijayraghavan U (2005). *OsMADS1*, a rice MADS-box factor, controls differentiation of specific cell types in the lemma and palea and is an early-acting regulator of inner floral organs. Plant J. 43(6):915-928.

Prasad K, Vijayraghavan U (2003). Double-stranded RNA interference of a rice *PI/GLO* paralog, *OsMADS2*, uncover its second whorl-specific function in floral organ patterning. Genetics 165(4):2301–2305.

Schmidt RJ, Ambrose BA (1998). The blooming of grass flower development. Curr. Opin. Plant Biol. 1(1):60-67.

Schmidt RJ, Veit B, Mandel MA, Mena M, Hake S, Yanofsky MF (1993). Identification and molecular characterization of *ZAG1*, the maize homolog of the *Arabidopsis* floral homeotic gene *AGAMOUS.* Plant Cell 5(7):729-737.

Schreiber DN, Bantin J, Dresselhaus T (2004). The MADS-box transcription factor *ZmMADS2* is required for anther and pollen maturation in maize and accumulates in apoptotic bodies during anther dehiscence. Plant Physiol. 134(3):1069-1079.

Theissen G, Becker A, Di Rosa A, Kanno A, Kim JT, Munster T, Winter KU, Saedler H (2000). A short history of MADS-box genes in plants. Plant Mol. Biol. 42(1):115-149.

Theissen G, Kim JT, Saedler H (1996). Classification and phylogeny of the MADS-box multigene family suggest defined roles of MADS-box gene subfamilies in the morphological evolution of eukaryotes. J. Mol. Evol. 43(5):484-516.

Theissen G, Strater T, Fischer A, Saedler H (1995). Structural characterization, chromosomal localization and phylogenetic evaluation of two pairs of *AGAMOUS*-like MADS-box genes from maize. Gene 156(2):155-166.

Thompson BE, Bartling L, Whipple C, Hall DH, Sakai H, Schmidt R, Hake S (2009). *bearded-ear* encodes a MADS-box transcription factor critical for maize floral development. Plant Cell 21(9):2578-2590.

Wang K, Tang D, Hong L, Xu W, Huang J, Li M, Gu M, Xue Y, Cheng Z (2010). *DEP* and AFO regulate reproductive habit in rice. PLoS Genet. 6(1):e1000818.

Wei B, Liu D, Guo J, Leseberg CH, Zhang X, Mao L (2013). Functional divergence of two duplicated D-lineage MADS-box genes *BdMADS2* and *BdMADS4* from *Brachypodium distachyon*. J. Plant Physiol. 170(4):424-431.

Whipple CJ, Ciceri P, Padilla CM, Ambrose BA, Bandong SL, Schmidt RJ (2004). Conservation of B-class floral homeotic gene function between maize and *Arabidopsis*. Development 131(24):6083-6091.

Wingen LU, Münster T, Faigl W, Deleu W, Sommer H, Saedler H, Theißen G (2012). Molecular genetic basis of pod corn (*Tunicate* maize). Proc. Natl. Acad. Sci. USA. 109(18):7115-7120.

Yamaguchi T, Lee DY, Miyao A, Hirochika H, An G, Hirano HY (2006). Functional diversification of the two C-class MADS-box genes *OsMADS3* and *OsMADS58* in *Oryza sativa*. Plant Cell 18(1):15-28.

Yanofsky MF, Ma H, Bowman JL, Drews GN, Feldmann KA, Meyerowitz EM (1990). The protein encoded by the *Arabidopsis* homeotic gene *agamous* resembles transcription factors. Nature 346(6279):35-39.

Yao SG, Ohmori S, Kimizu M, Yoshida H (2008). Unequal genetic redundancy of rice *PISTILLATA* orthologs, *OsMADS2* and *OsMADS4*, in lodicules and stamen development. Plant Cell Physiol. 49(5):853-857.

Yoshida H, Itoh J, Ohmori S, Miyoshi K, Horigome A, Uchida E, Kimizu M, Matsumura Y, Kusaba M, Satoh H, Nagato Y (2007). *superwoman1-cleistogamy*, a hopeful allele for gene containment in GM rice. Plant Biotechnol. J. 5(6):835-846.

Zahn LM, Kong H, Leebens-Mack JH, Kim S, Soltis PS, Landherr LL, Soltis DE, Depamphilis CW, Ma H (2005). The evolution of the *SEPALLATA* subfamily of MADS-box genes: a preangiosperm origin with multiple duplications throughout angiosperm history. Genetics 169(4):2209-2223.

Zahn LM, Leebens-Mack JH, Arrington JM, Hu Y, Landherr LL, dePamphilis CW, Becker A, Theissen G, Ma H (2006). Conservation and divergence in the *AGAMOUS* subfamily of MADS-box genes: evidence of independent sub- and neofunctionalization events. Evol. Dev. 8(1):30-45.

Zhao Q, Weber AL, McMullen MD, Guill K, Doebley J (2011). MADS-box genes of maize: frequent targets of selection during domestication. Genet. Res. 93(1):65-75.