



Review

The B_{sister} MADS-box proteins have multiple regulatory functions in plant development

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ABSTRACT

B_{sister} MADS-box proteins are a group of recently characterized MADS family transcription factors. The genes encoding these proteins have a close relationship with the male-organ-expressed class B floral homeotic genes, but are predominantly expressed in female organs. B_{sister} MADS-box proteins display important regulatory functions in seed coat development, fruit development, and proanthocyanidin biosynthesis. Therefore, genes encoding B_{sister} MADS-box proteins are potentially useful in genetic engineering of crop plants to reduce seed coat thickness and condensed tannin content. In this review, recent progress on biochemical, molecular and functional aspects of plant B_{sister} MADS-box proteins is discussed.

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1. Introduction

MADS-box proteins are a large group of transcription factors containing a highly conserved MADS domain, which is named after the characterization of four proteins in this group, MINICHROMOSOME MAINTENANCE 1, AGAMOUS, DEFICIENS and SERUM RESPONSE FACTOR (Gramzow and Theißen, 2010). Plant MADS-box genes are divided into type I and type II groups based

on the corresponding amino acid sequence of the MADS domain (Becker and Theißen, 2003). Type I MADS-box genes are composed of three subgroups, M α , M β , and M γ , and the type II genes are further subdivided into two subgroups, MIK^C and MIK* (Gramzow and Theißen, 2010; Becker and Theißen, 2003). In addition, MADS-box genes are the major members of plant floral organ identity genes, which have been divided into five classes according to the ABCDE model (Krizek and Fletcher, 2005). MADS-box proteins are involved in controlling diverse physiological processes including male and female gametophyte development, plant hormone response, seed development, flowering time determination and vernalization response (Melzer and Theißen, 2011). Recently, a novel type II MIK^C MADS-box gene subfamily with a sister-group relationship with class B floral homeotic genes

Abbreviations: ABS, *Arabidopsis B_{sister} gene*; AGL, AGAMOUS-LIKE; FBP24, *Floral Binding Protein24*; GOA, GORDITA; ORF, open reading frame; PA, proanthocyanidin; SEP, SEPALLATA; TT16, TRANSPARENT TESTA 16

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was identified and named B_{sister} MADS-box genes (Becker et al., 2002). Although only a few B_{sister} MADS-box proteins have been characterized in detail, these transcription factors have important regulatory functions in seed coat and fruit development, and condensed tannin biosynthesis (de Folter et al., 2006; Erdmann et al., 2010; Nesi et al., 2002; Prasad et al., 2010). Therefore, a comprehensive understanding of these proteins and their physiological functions would be valuable for breeding programs and agricultural biotechnology.

2. Plant B_{sister} MADS box proteins and their interactors

2.1. Discovery

The B_{sister} MADS-box gene subfamily was first identified by Becker et al. in 2002 (Becker et al., 2002). Subsequently, two B_{sister} genes, *Arabidopsis B_{sister} gene* (*AtABS*, also known as *AGAMOUS-LIKE 32*, *AGL32*) and *Petunia hybrida Floral Binding Protein24* (*PhFBP24*) were studied in detail (de Folter et al., 2006; Nesi et al., 2002; Kaufmann et al., 2005). *AtABS* is also known as *Arabidopsis TRANSPARENT TESTA 16* (*AtTT16*) because the seeds of *AtTT16* null mutant lines have light yellow color (Nesi et al., 2002; Koornneef, 1990). Since *AtABS*, *AGL32*, and *AtTT16* are all names for the same gene (*At5g23260*), we will consistently use *AtTT16* throughout this paper. *AtTT16* was shown to function in the regulation of endothelium development and anthocyanidin production (Nesi et al., 2002). Recently, a young paralog gene of *AtTT16*, *Arabidopsis GORDITA* (*AtGOA*, formerly known as *AGL63*) was characterized (Erdmann et al., 2010; Prasad et al., 2010). Some of the known B_{sister} MADS-box genes are listed in Fig. 1A.

2.2. Gene structure and expression patterns

AtTT16 is encoded by an 1899 bp gene that consists of six exons and five introns. The cDNA length is 759 bp. *AtGOA* gene is 256 bp shorter than *AtTT16* gene and consists of five exons. The open reading frame (ORF) of *AtGOA* is 648 bp. *AtTT16* homologs have been identified in both monocot and dicot plants, but interestingly, *AtGOA* is currently only found in the sequenced genome of Brassicaceae (Erdmann et al., 2010).

Both *AtTT16* and *AtGOA* are predominantly expressed in reproductive organs. *AtTT16* expression has been detected in buds, mature flowers, and developing seeds but was absent from vegetative parts such as silique valves, seedlings, leaves, stems, and root samples (Becker et al., 2002; Nesi et al., 2002). de Folter et al. (2006) studied the expression of *PhFBP24* in *Petunia* by Northern blot, and found that *PhFBP24* was expressed predominantly in ovary but not in vegetative tissues or other floral organs. In addition, the expression of *PhFBP24* during ovule development was further studied by *in situ* hybridization. *PhFBP24* expression was detected in very young ovule primordia, then in the nucellus and the integument in developing ovule, and finally in the endothelium in mature ovule (de Folter et al., 2006). It should be noted that *Petunia* has only one integument, whereas *Arabidopsis* has two (de Folter et al., 2006). *AtGOA* was detected in both vegetative and reproductive organs by quantitative real-time PCR, but the expression level in the latter is much higher than that in the former (Erdmann et al., 2010). Expression of *AtGOA* was detected in ovules, sepals, stamens, style, replum and carpel walls, and embryos by GUS staining and *in situ* hybridization (Erdmann et al., 2010; Prasad et al., 2010). In addition, *AtGOA* expression was detected in outer integuments but not in the endothelium layer where *AtTT16* is presumably expressed, which was consistent with the additive roles of *AtGOA* and *AtTT16* in seed coat development.

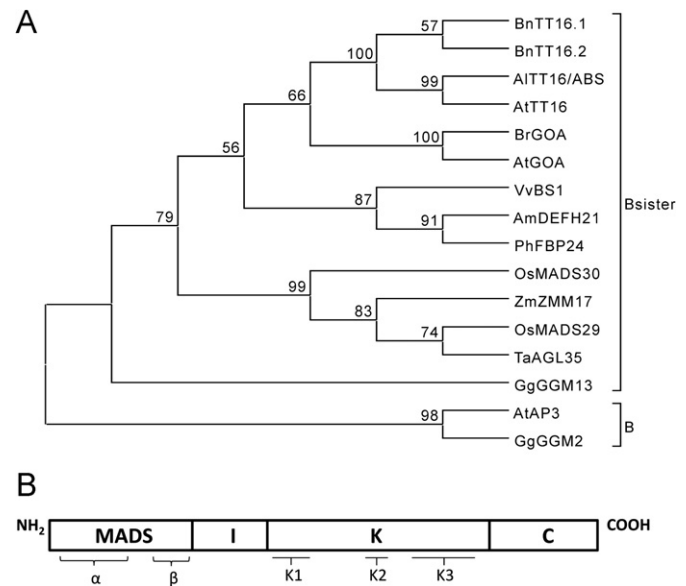


Fig. 1. Plant B_{sister} MADS-box genes. (A) Phylogenetic tree based on an alignment of B_{sister} MADS-domain genes using B group MADS-box genes as the out-group (*AtAP3*, *GgGGM2*). Protein-based cDNA alignments of known MADS-Box proteins were produced using the RevTrans1.4 server (Wernersson and Pedersen, 2003). Evolutionary analyses were conducted using the Maximum Likelihood method based on the Tamura–Nei model method in MEGA5. Bootstrap values (percent) were obtained with 1000 replications and are shown at the nodes. *AtAP3*, *Arabidopsis thaliana* NP191002.1; *AIT16/ABS*, *Arabidopsis lyrata* EFH48305.1; *AmDEFH21*, *Antirrhinum majus* CAC85225; *GOA*, *Arabidopsis thaliana* AAN52807.1; *TT16*, *Arabidopsis thaliana* CAC85664.1; *BnTT16.1*, *Brassica napus* ABY59773.1; *BnTT16.2*, *Brassica napus* ABY59774.1; *BrGOA*, *Brassica rapa* Bra023162; *GgGGM13*, *Gnetum gnemon* CAB44459; *GgGGM2*, *Gnetum gnemon* CAB44448.1; *OsMADS29*, *Oryza sativa* Q6H711; *OsMADS30*, *Oryza sativa* AAO39706; *FBP24*, *Petunia hybrida* AAK21255.1; *TaAGL35*, *Triticum aestivum* ABF57953.1; *VvBS1*, *Vitis vinifera* CBI27190.3; *ZmZMM17*, *Zea mays* CAC81053. (B) Domain structure of type II MIKC-type MADS box proteins (modified after Kaufmann et al., 2005). K1, K2, K3 indicate the positions of the K1–K3 α -helices.

2.3. Protein structures and interactions

Similar to other typical MIKC-type MADS-box proteins, most of the B_{sister} proteins contain four domains comprising MADS (M), intervening (I), keratin-like (K) and C-terminal (C) domains (Fig. 1B). In general, the MADS domain is highly conserved and exhibits DNA binding, dimerization, and nuclear localization functions (Becker and Theißen, 2003). The I domain is relatively weakly conserved and may be implicated in functional specificity of MADS proteins (Becker et al., 2002). The conservative K domain is characterized by three strings of heptad repeats (K1, K2 and K3), which are proposed to fold into three amphipathic α -helices involved in protein–protein interactions among MADS proteins (Yang and Jack, 2004). The C domain is the most variable region and is involved in transcriptional activation, and/or the formation of multimeric transcription factor complexes. The *AtGOA* protein has a different structure from the canonical B_{sister} proteins: it has a shorter C domain which has no conserved motif and a loss of part of the K domain (K2 and K3) (Erdmann et al., 2010). The deviant C domain, however, may form an α -helix that is required for protein interactions (Erdmann et al., 2010).

MIKC-type transcription factors are known to interact with protein partners, especially with other MADS members, to form functional complexes (Kaufmann et al., 2005). *AtTT16* can form dimers with E-type plant floral organ identity proteins (according to the ABC model) *Arabidopsis* *SEPALLATA1* (*AtSEP1*), *AtSEP2* and *AtSEP3* (Kaufmann et al., 2005). *AtTT16* can also form a higher order protein complex including B_{s} –D–E complexes with *Arabidopsis* *SEEDSTICK* (D-type) and *SEP2/SEP3* (E-type) proteins and

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