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REVIEW

# *BABY BOOM* (*BBM*): a candidate transcription factor gene in plant biotechnology

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**Abstract** Plants have evolved a number of transcription factors, many of which are implicated in signaling pathways as well as regulating diverse cellular functions. *BABY BOOM* (*BBM*), transcription factors of the AP2/ERF family are key regulators of plant cell totipotency. Ectopic expression of the *BBM* gene, originally identified in *Brassica napus*, has diverse functions in plant cell proliferation, growth and development without exogenous growth regulators. The *BBM* gene has been implicated to play an important role as a gene marker in multiple signaling developmental pathways in plant development. This review focuses on recent advances in our understanding of a member of the *AP2* family of transcription factor *BBM* in plant biotechnology including plant embryogenesis, cell proliferation, regeneration, plant transformation and apogamy. Recent discoveries about the *BBM* gene will inevitably help to unlock the long-standing mysteries of different biological mechanisms of plant cells.

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**Keywords** *BABY BOOM* (*BBM*) · Cell proliferation · Embryogenesis · Transformation

**Abbreviations**

| | |
|---|---|
| *ABI3* | *Abscisic acid insensitive 3* |
| *AP2* | *APETALA2* DNA-binding domain in plant proteins |
| *BBM* | *BABY BOOM* |
| CHX | Cycloheximide |
| CRE | Creates recombination |
| DEX | Dexamethasone |
| ERF | Ethylene-responsive element binding factor |
| *FUS3* | *FUSCA3* |
| GR | Glucocorticoid receptor |
| GUS | $\beta$-Glucuronidase |
| *LEC* | *LEAFY COTYLEDON* |
| ORF | Open reading frame |
| *PKL* | *PICKLE* |
| *PRC* | *Polycomb repressive complex* |
| RACE | Rapid amplification of cDNA ends |
| RT-PCR | Real-time-polymerase chain reaction |
| SE | Somatic embryogenesis |
| TAA1 | Tryptophan aminotransferase of *Arabidopsis* 1 |
| *WUS* | *WUSCHEL* |

## Introduction

The ability to regenerate new tissue, organs (pluripotency) or embryos (totipotency) via tissue culture is a much-applied phenomenon in plant biotechnology. In vitro plant regeneration is an important model system in modern crop breeding and has remarkable potential for biotechnological application. The genetic basis for changes in in vitro regeneration potential still remains unclear. However, studies on the genetic mechanisms that control in vitro regeneration suggest that a number of transcription factor genes which have been identified, are specifically activated or differentially expressed during plant embryogenesis when somatic cells are converted into embryonic cells (Chugh and Khurana 2002; Boutilier et al. 2002; Rojas-Herrera et al. 2002; Schrader et al. 1997; Hu et al. 2005; Rupps et al. 2016; Zhai et al. 2016). Among the genes involved in plant embryogenesis, the *BABY BOOM* (*BBM*) gene has an important role (Boutilier et al. 2002). The *BBM* gene, which is preferentially expressed, activates a signal transduction pathways leading to the induction of differentiated somatic cells and somatic embryo formation (Boutilier et al. 2002). The *BBM* gene encodes the APETALA2 (AP2) FAMILY/ETHYLENE-RESPONSIVE ELEMENT BINDING FACTOR (AP2/ERF) domain transcription factor, which has diverse functions in cell proliferation, plant growth and development (Riechmann and Meyerowitz 1998; Nole-Wilson et al. 2005; Feng et al. 2005; Floyd and Bowman 2007; Passarinho et al. 2008; Ouakfaoui et al. 2010) (Table 1). The *BBM* gene was first isolated as a marker from embryogenic cells in microspore-derived tissue culture and was shown to induce somatic embryos when ectopically expressed in *Brassica napus* (Boutilier et al. 2002). The *BBM* gene induces embryogenesis in differentiated cells under culture conditions that normally do not support in wild-type plants and possibly acts as a key regulator of plant embryonic development (Boutilier et al. 2002). The role of the *BBM* gene has been linked to plant embryogenesis in many plant species such as *Arabidopsis thaliana* (Boutilier et al. 2002), *Brassica napus* (Boutilier et al. 2002), *Glycine max* L. (Ouakfaoui et al. 2010), *Capsicum annuum* L. (Irikova et al. 2012) and *Zea mays* (Salvo et al. 2014). The *BBM* gene acts as a possible biomarker and is involved in multitasking functions including cell proliferation, shoot formation, somatic embryogenesis (SE) induction, development, promoting apogamy and stimulating transformation (Boutilier et al. 2002; Passarinho et al. 2008; Heidmann et al. 2011; Lowe et al. 2016; Horstman et al. 2017a; Bui et al. 2017) (Fig. 1). However, the molecular mechanism which regulates these biological functions is not clear. As shown in Fig. 1, several regulatory genes such as *PICKLE* (*PKL*) and *Polycomb repressive complex1/2* (*PRC1/2*) subsequently induce the *BBM* transcription factor gene. The *BBM* gene transcriptionally regulates *LEAFY COTYLEDON1* (*LEC1*), *LEAFY COTYLEDON2* (*LEC2*) and *AGAMOUS-LIKE15* (*AGL15*) genes during SE to promote embryonic competence. *LEC1* expressed the *YUC* gene, which encodes a biosynthesis enzyme, whereas *LEC2* and *AGL15* induces the *IAA30* (negative regulator of auxin signaling) (Braybrook et al. 2006; Zheng et al. 2009; Kumar and Van Staden 2017). In addition, the *BBM* gene binds to *TAA1* and *YUC* gene, which encodes an auxin biosynthesis enzyme (Horstman et al. 2017a). To the best of our knowledge, there is no review available on *BBM* transcription factor gene. The main objective of this review is to present a brief update on the current status and recent advances in understanding the diverse functions of the *BBM* gene and provide insights into the discovered *BBM* gene functions in plant embryogenesis, growth and development.

## *BBM* transcription factor is a key marker gene in plant embryogenesis

The developmental pathway of SE involves complex cellular reprogramming and activation of various signaling pathways. A number of molecular genetics studies suggest that ectopic expression of transcription factor genes induce spontaneous SE (Salvo et al. 2014; Horstman et al. 2017a, b). The *BBM* transcription factor gene is a key regulator of plant cell totipotency, which is ectopically expressed and induces SE without exogenous plant growth regulators or stress (Boutilier et al. 2002; Horstman et al. 2017a). Ectopic expression of the *BBM* gene stimulated signaling pathways that promoted cell division and dedifferentiation. However, this process was not dependent on the addition of auxin/cytokinin but could be improved with the addition of these plant growth regulators (Boutilier et al. 2002).

**Table 1** Showing *BBM* and *BBM*-like reported gene from different plant species and their biological functions in plant growth and development

| Plant species | Eudicot/monocot | Gene type | Name of gene | Biological function | References |
|---|---|---|---|---|---|
| *Brassica napus* | Eudicot | *BBM* | *BnBBM* | Cell proliferation, morphogenesis during embryogenesis | Boutilier et al. (2002) |
| *Arabidopsis thaliana* | Eudicot | *BBM* | *AtBBM* | Cell proliferation, spontaneous formation of somatic embryos, cotyledon-like structures on seedlings | Boutilier et al. (2002) |
| *Arabidopsis thaliana* | Eudicot | *BBM* | *BBM:GR* | Activates a complex developmental pathways into cell proliferation and cell growth | Passarinho et al. (2008) |
| *Arabidopsis thaliana* | Eudicot | *BBM* | *BBM* | Cell proliferation and somatic embryogenesis | Kulinska-Lukaszek et al. (2012) |
| *Arabidopsis thaliana* | Eudicot | *BBM* | *BBM:GR* | Improve plant regeneration and yield fertile plants | Lutz et al. 2015 |
| *Nicotiana tabacum* L. | Eudicot | *BBM* | *AtBBM; BnBBM* (heterologous gene) | Cell proliferation and differentiation | Srinivasan et al. (2007) |
| *Glycine max* L. | Eudicot | *BBM* | *GmBBM* | Somatic embryogenesis and embryo development | Ouakfaoui et al. (2010) |
| *Rosa canina* | Eudicot | *BBM* | *RcBBM1* *RcBBM2* | Improve shoot regeneration efficiency | Yang et al. (2014) |
| *Theobroma cacao* | Eudicot | *BBM* | *TcBBM* | Enhance somatic embryogenesis without compromising plant growth and development | Florez et al. (2015) |
| *Capsicum annuum* | Eudicot | *BBM* | *BnBBM* | Used to efficiently regenerate transgenic plants through *Agrobacterium*-mediated transformation | Heidmann et al. (2011) |
| *Coffeaarabica* | Eudicot | *BBM* | *CaBBM* | *In vitro* embryogenic process | Silva et al. (2015) |
| *Sorghum bicolor* | Monocot | *BBM* | *Maize BBM* | Improve transformation efficiency | Lowe et al. (2016) |
| *Saccharum officinarum* | Monocot | *BBM* | *Maize BBM* | Improve transformation efficiency | Lowe et al. (2016) |
| *Oryza sativa* | Monocot | *BBM* | *Maize BBM* | Improve transformation efficiency | Lowe et al. (2016) |
| *Sorghum bicolor* | Monocot | *BBM* | *Maize BBM* | Effiecient *Agrobacterim*-mediated transformation | Mookan et al. (2017) |
| *Musa acuminata* | Monocot | *BBM* | *MaBBM1* *MaBBM2* | Induction of somatic embryogenesis | Shivani et al. (2017) |
| *Pennisetum glaucum* | Monocot | *BBM* | *PsASGR-BBML* | Induction of apomixis | Conner et al. (2015) |
| *Ceratopteris richardii* | Fern | *BBM* | *BnBBM* | Promote apogamy | Bui et al. (2017) |

In *Brassica napus*, two *BBM* genes (*BnBBM1* and *BnBBM2*) and in *Arabidopsis thaliana* a single ortholog (*AtBBM*) were identified. Overexpression of these genes revealed enhanced cell proliferation and morphogenesis during embryogenesis (Boutilier et al. 2002). *Brassica* and *Arabidopsis* plants transformed with *UBI::BBM* and *35S::BBM* constructs respectively produced cotyledon-like somatic embryos on post germination organs. In addition, ectopic *BBM* expression induced a variety of different pleiotropic

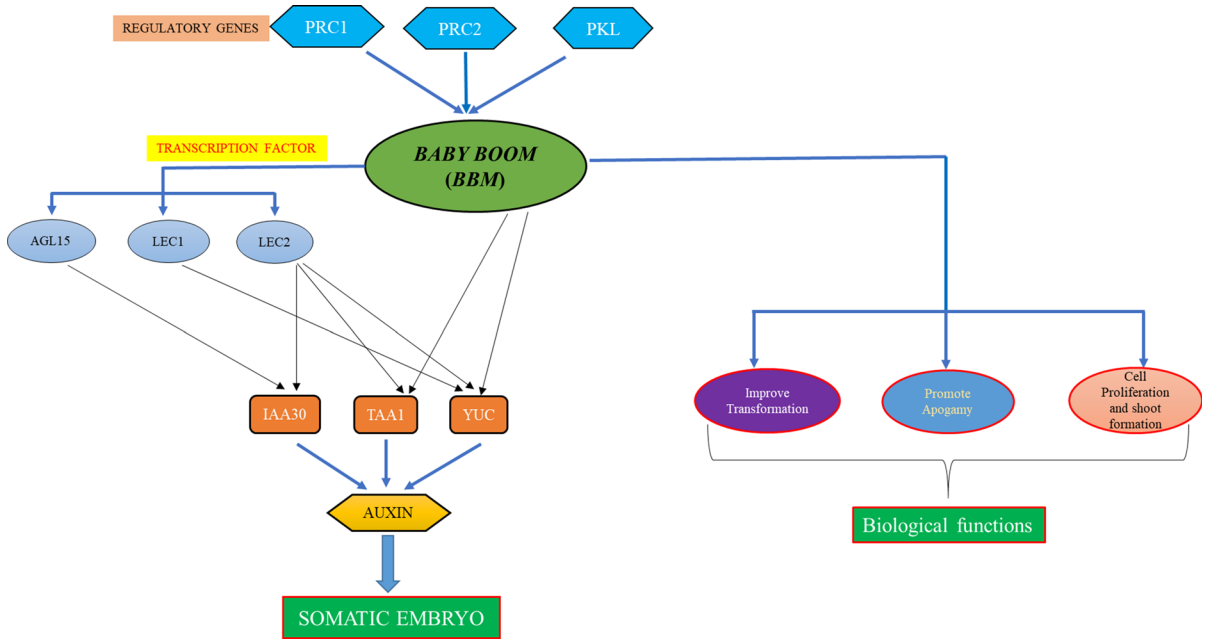


**Fig. 1** Schematic overview of the *BABY BOOM* (*BBM*) transcription factor gene that may regulate diverse functions of plant growth and development

phenotypes such as pinched or lobed cotyledons, thickened or callused hypocotyls, short shoots, formation of ectopic shoots, callus formation and anthocyanin accumulation on vegetative and regenerative development at a low penetrance in *UBI::BBM* and *35S::BBM Brassica* and *Arabidopsis* transgenic seedlings respectively. However, these phenotypes were variable within and between *Brassica* and *Arabidopsis* transgenic lines (Boutilier et al. 2002). These results suggest that the *BBM* gene regulates signaling pathways for SE and act as a plant hormone stimulator.

Overexpression of *BBM*-mediated SE enhanced plant regeneration in *Populus tomentosa* (Deng et al. 2009). Ectopic expression of *BBM* induced somatic embryos formation from Chinese white poplar callus. A total of 12 somatic embryos were induced from 6 calli after 4 weeks of culture. Out of these 12, only 6 somatic embryos were germinated and converted into plantlets (Deng et al. 2009).

The *BBM* gene is also involved in SE and embryo development in *Glycine max* L. (soyabean) (Ouakfaoui et al. 2010). Three AP2 gene families, *GmBBM1*, *GmAIL5* and *GmPLT2* were identified and isolated from embryonic cultures of *Glycine max* L. (soybean). The *GmBBM1* sequence showed high similarity (> 91%) to *AtBBM* and *BnBBM* genes, whereas *GmAIL5* and *GmPLT2* were similar to *Arabidopsis AINTEGUMENTA-like* (*AIL5*) and *PLETHORA2* (*PLT2*) respectively. Sequence comparison of *BBM* orthologues identified the presence of five motifs in the N-terminal, and five motifs in the C-terminal sequences. In the N-terminal sequences, the fourth motif (*bbm-1*) was specific to *BBM*-like genes, whereas in the C-terminal sequences, all five motifs were conserved with a low level of specificity. The function of the *bbm-1* sequence motif in SE and embryo development regulation was further detected by deletion and domain swap analysis. Further examination indicated that, *bbm-1* was linked to the one other euANT2 motif, which was identified in the euANT lineage including *PLT2* and *AIL5* genes. A deletion of the euANT2 motif singly and together with *bbm-1* prevented somatic embryos from generating shoots after prolonged times in culture (Ouakfaoui et al. 2010). These results provide an understanding of the mechanism by which *BBM* governs embryogenesis.

In *Theobroma cacao*, a *BBM* gene (*TcBBM*) was cloned and expressed to promote the transition of somatic *T. cacao* cells from vegetative to embryonic growth (Florez et al. 2015). The *TcBBM* expression level was observed throughout the embryo

development; globular, heart, early torpedo, late torpedo and mature somatic embryo stages. Overexpression of *TcBBM* in *T. cacao* led to phenotype, which did not require exogenous hormones for direct embryogenesis. However, transient expression of *TcBBM* improved embryogenic potential. These results indicated that *TcBBM* has an important role in SE and its transcription level could serve as a biomarker for embryonic growth in *T. cacao* tissue (Florez et al. 2015).

In a recent report, Horstman et al. (2017a) demonstrated that the *BBM* gene works as a major regulator for plant cell totipotency. *BBM* transcriptionally regulated *LEC1/2*, *FUSCA3* (*FUS3*) and *ABSCISIC ACID INSENSITIVE* (*ABI3*) gene networks. These results also suggested that *LEC2* and *ABI3* are positive regulators of *BBM*-mediated embryogenesis, where as *LEC1* and *FUS3* are essential for SE. *BBM*-induced SE is a dose and context-dependent mechanism. High *BBM* doses induce SE, whereas lower doses induce organogenesis. However, no cell differentiation was found in the lowest *BBM* dose. This study also hypothesized that *BBM*-mediated embryogenesis was enhanced by *LAFL* gene expression (Horstman et al. 2017a). The *BBM* gene has emerged as important transcription factor that control embryogenesis and has considerable potential in plant biotechnology. These results suggest that the *BBM* gene acts as a key regulator for plant cell totipotency and plant embryo identity. In addition, it provides new insight into the molecular mechanism by which the *BBM* gene controls SE. However, the exact mechanism of the *BBM* gene controlling signaling transmission specificity to regulate somatic embryo formation remains unclear.

## *BBM* transcription factor enhances cell proliferation and regeneration

Overexpression of native and heterologous *BBM* genes are also responsible for the induction of cell proliferation and regeneration in different plant species (Srinivasan et al. 2007; Morcillo et al. 2007; Passarinho et al. 2008; Bandupriya et al. 2014; Yang et al. 2014; Lutz et al. 2015) It has also been used to promote apogamy in ferns (Bui et al. 2017).

The *BBM* gene is expressed as a marker and activates a complex signaling network of different developmental pathways linked to cell proliferation and growth (Passarinho et al. 2008). By using DNA microarray analysis in combination with post-translationally regulated BBM:GR protein and cycloheximide (CHX), a number of target genes have been identified which are directly activated by *BBM* gene expression. A number of target genes encoding proteins have been shown to be expressed and involved in cellular signaling and cell wall modifications (Passarinho et al. 2008).

Srinivasan et al. (2007) examined the ectopic expression of *BBM* on tobacco (*Nicotiana tabacum*) development and regeneration capacity. Eight transgenic tobacco lines expressed the *35S::AtBBM* construct and twenty transgenic tobacco lines expressing the *35S::BnBBM* construct. They exhibited a number of similar phenotypes including leaf rumpling, callus formation and sterility. However, no adventitious shoot formation and somatic embryo formation was observed on the *35S::BBM* tobacco lines (Srinivasan et al. 2007).

Two *BBM* orthologue genes *RcBBM1* and *RcBBM2* were isolated by a combination of degenerate PCR and RACE from *Rosa canina* (Yang et al. 2014). The sequence analysis revealed that the *RcBBM1* (2936 bp in length) encodes a predicted protein of 832 amino acids and comprises an ORF of 2499 bp, whereas *RcBBM2* (2921 bp in length) contained an ORF of 2487 bp and encodes a predicted protein of 828 amino acids. Both genes showed as candidate markers for improving shoot regeneration capacity in *R. canina*. By using confocal microscopic examination, it was revealed that RcBBM1 and RcBBM2 were both nucleus-localized proteins. The overexpression of *RcBBM1* and *RcBBM2* transgenic line in *A. thaliana* was characterized in shoot regeneration and SE using RT-PCR (Yang et al. 2014). The results suggested that *RcBBM1* and *RcBBM2* are candidate genes for promoting shoot regeneration capacity in *R. canina*, allowing further research on *RcBBMs* in spontaneous production of somatic embryos.

Lutz et al. (2015) described novel improved plant regeneration in *A. thaliana* through a steroid-inducible *BBM* system that resulted in fertile and diploid plants. Two steroid-inducible BBM constructs BBM:GR and BBM:GFP:GR were created. The BBM coding region fused with the glucocorticoid receptor (GR) steroid-binding domain and BBM:GFP:GR fusion facilitated the visualization of BBM movement. In the absence of synthetic steroid dexamethasone (DEX), the BBM:GR

fusion protein was localized in the cytoplasm. However, in the presence of DEX in the culture medium, *BBM* transcription factor translocated from the cytoplasm to the nucleus, hence activating genes involved in embryogenesis. In the presence of DEX, the leaf section produced shoots and callus whereas, removal of DEX allowed seed formation and flowering. However, few shoot regeneration was observed in the absence of DEX using flow cytometry. Increased ploidy levels were also noted in the regenerated plants (Lutz et al. 2015). Together, these results indicated that the *BBM* gene plays an essential role in cell proliferation and regeneration. The *BBM* gene regulated a complex network of developmental pathways associated with cell proliferation and regeneration. In addition, the *BBM* gene was found as a candidate marker for improving shoot regeneration efficiency.

## *BBM* transcription factor gene is crucial in plant transformation

Plant transformation is commonly mediated by *Agrobacterium*, where protoplast and particle bombardment has enabled novel insights into plant biology. Standard plant transformation is hampered by long turnaround times to recover transgenic plants as well as several technical bottlenecks (Altpeter et al. 2016; Mookan et al. 2017). Recent research reports offer a promising breakthrough solution to many obstacles where plant transformation is improved using morphogenic regulators to mediate transformation (Heidmann et al. 2011; Lowe et al. 2016; Svitashev et al. 2016; Mookan et al. 2017).

The overexpression of the *BBM* gene has been used as a biotechnology tool to improve transformation in model and crop species (Deng et al. 2009; Heidmann al. 2011; Lutz et al. 2011; Florez et al. 2015; Lowe et al. 2016). The ectopic expression of *B. napus BBM* (*BnBBM*) transcription factor was used to efficiently regenerate transgenic plants from *Capsicum annuum* (Sweet pepper) varieties (Heidmann et al. 2011). The *C. annuum* explants were co-cultivated with the *35S:BnBBM:GR* construct carrying the *GUS* selectable marker and this improved transformation efficiency for each of the pepper (Fiesta, Ferrari and Spirit) varieties. Out of three pepper varieties, transgenic plantlets were produced for only two varieties (Fiesta and Ferrari). However in control experiments, no transgenic plantlets were obtained from any pepper variety. Average transformation efficiency 0.6 and 1.1% were obtained for Fiesta and Ferrari pepper varieties, respectively (Heidmann et al. 2011).

Overexpression of the *BBM* gene was used to produce transgenic *Populus tomentosa* (Chinese white poplar) (Deng et al. 2009). *BBM* overexpression developed somatic embryos from Chinese white poplar calli, which were converted into plantlets. However, no regeneration was obtained from untransformed calli. To produce marker-free lines, the system was combined with heat shock-inducible FRT/FLP (site-specific recombination system from *Saccharomyces cerevisiae*) system (Deng et al. 2009). This study also confirmed that the *BBM* gene acts as a positive selectable marker for Chinese white poplar transformation, and transgenic poplar plants can be obtain without the use of any antibiotic or herbicide resistance genes (Deng et al. 2009).

In a promising breakthrough report by Lowe et al. (2016) the *BBM* gene was shown to improve monocot transformation in several commercial genotypes. Overexpression of *Zea mays* (maize) *BBM* gene and *WUSCHEL2* (*WUS2*) stimulated transformation frequency in *Saccharum officinarum* (sugarcane) callus, *Oryza sativa* ssp. *Indica* (rice) callus and *Sorghum bicolor* (sorghum) immature embryos. The *BBM* gene transformed directly into leaf segment from seedlings or embryo from mature seeds in a variety of pioneer inbred lines (PHH5G). The recovery of one inbred maize line without the use of a selectable marker was also reported. These results indicated a dramatic increase in transformation frequencies through overexpression of *BBM* and *WUS2* and a strong dependence on the promoters used to drive the *BBM* and *WUS2* morphogenic regulators (Lowe et al. 2016).

More recently, by using co-expression of maize *BBM* and *WUS2* transcription factor genes, an efficient *Agrobacterium*-mediated transformation was identified in sorghum without the use of a chemical selectable marker (Mookan et al. 2017). In addition, a reliable and increased transformation frequency was established for of the recalcitrant B73 (maize inbred) and sorghum (P898012 genotypes) varieties via co-expression of *BBM* and *WUS*. The PHP78891 vector comprised *CRE:WUS2:BBM* cassette, bracketed by *lox* P sites. Transgenic introduction of this expression vector showed transient expression of *GFP* in early and late somatic embryos, shoots, vegetative organs

and pollen. By using molecular analysis (PCR and southern blotting), regenerated maize B73 and sorghum P898012 plants were confirmed to be transgenic. A significantly increased transformation frequency for B73 (15%) and P898012 genotypes (6.2%) were noted without the use of a selectable marker (Mookan et al. 2017). These results indicated that technology for plant transformation is entering a new era and these results can extend the use of transient expression of morphogenic regulators without a selectable marker to overcome transformation barriers. In future, the role of *BBM* gene would increase the knowledge in unknown signaling pathways stimulating transformation.

## *BBM*-mediated apogamy

In plants, naturally occurring mode of asexual reproduction through non-zygotic embryogenesis is known as apogamy. This allows reproduction via seeds without meiosis and fertilization (Nogler 1984; Tucker et al. 2003; Bui et al. 2017).

In *Pennisetum glaucum* (pearl millet), *PsASGR-BABY BOOM-LIKE* (*PsASGR-BBML*) is expressed as a marker gene for apomixis (Conner et al. 2015). By using RT-PCR, it was demonstrated that the *PsASGR-BBML* gene is expressed in egg cells, which induce parthenogenesis before fertilization and also produce the haploid offspring in transgenic pearl millet (Conner et al. 2015). This study also suggested that *PsASGR-BBML* plays a significant role as a transcription factor to promote parthenogenesis and embryo development without fertilization.

In a recent promising report, ectopic expression of the *BBM* gene was shown to promote apogamy in a non-vascular plant *Ceratopteris richardii* (Bui et al. 2017). Ectopic expression of *B. napus BBM* (*BnBBM*) transgene in *C. richardii* promoted spontaneous production of apogamy without sugar supplement. In *C. richardii*, the *BnBBM* gene was ectopically expressed using an *Agrobacterium*-mediated transformation and spontaneous apogamy was observed in transgenic gametophytes. Overexpression of *BnBBM* showed various phenotypic effects on gametophyte generations such as increased transformation efficiency, cordate shape deviation of gametophytes and callus induction. In the sporophyte generation, *BnBBM* expression resulted in adventitious shoot development and excess in shoot regeneration. *CrANT*, (a fern homolog of the *Arabidopsis ANT* gene), knockdown reduced the gametophyte response to sugar-induced apogamy (Bui et al. 2017). These results indicated that *BnBBM* promote cell differentiation and trigger developmental pathways in *C. richardii*. In future, more comprehensive analysis may provide new insights to decipher the puzzle of molecular mechanism underlying in apogamy.

## Conclusions and future perspectives

*BBM* transcription factor has emerged as an important gene marker that controls diverse aspects of plant growth and development and has considerable potential for plant biotechnological application. Many research reports on the precise expression of the *BBM* gene provides novel evidence on its role in plant embryogenesis. We also note that there is clear evidence that the *BBM* gene exerts distinct functions in different physiological and developmental signaling pathways. In this review, we emphasized diverse functions of plant cell proliferation, growth and development regulated by *BBM* gene. The *BBM* gene acts as a candidate gene marker to participate in diverse developmental responses and signaling pathways, but it is still unclear how the *BBM*-mediated signaling pathways determine specificity. In addition, how the *BBM* gene controls signaling transmission specificity to regulate somatic embryo formation, cell differentiation, plant growth and transformation remains unclear.

Future research will be required on the efficient transformation system to better understand *BBM* gene function. This should further reveal the individual target gene functions to determine the transformation efficiency, somatic embryo induction, plant growth and development. Further investigations of the *BBM* gene would increase knowledge in unknown signaling pathways, will open new avenues into the activation mechanisms and provide new insights on the signaling specificity. It would also help in a better understanding of the complex interaction of gene regulation and other roles of the *BBM* gene in plant cells.

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**Compliance with ethical standards**

**Conflict of interest** The authors declare that they have no conflict of interest.

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