Plant Gene and Trait 2026, Vol.17, No.3, 173-181
http://genbreedpublisher.com/index.php/pgt

Review Article **Open Access**

MADS-Box Transcription Factors in *Arabidopsis thaliana*: Molecular Control of Floral Organ Identity and Development

Rimjhim Chandra
Department of Botany, Government Degree College, Chamba, Himachal Pradesh, 176314, India
Corresponding email: rimjhimchandra6@gmail.com

Plant Gene and Trait, 2026, Vol.17, No.3 doi: 10.5376/pgt.2026.17.0012
Received: 17 Apr., 2026
Accepted: 15 May, 2026
Published: 3 Jun., 2026

Preferred citation for this article:
Chandra R, 2026, MADS-box transcription factors in *Arabidopsis thaliana*: molecular control of floral organ identity and development, Plant Gene and Trait, 17(3): 173-181 (doi: 10.5376/pgt.2026.17.0012)

Abstract MADS-box transcription factors are central regulators of plant development, particularly in reproductive processes. This review integrates molecular, phylogenetic, transcriptomic, and functional analyses of the complete MADS-box gene family in *Arabidopsis thaliana*. These transcription factors regulate gene expression through binding to CArG-box cis-elements, with specificity determined by combinatorial protein interactions and higher-order complex formation. Genome-wide studies reveal diversification of MADS-box genes into distinct lineages with specialized developmental roles. Transcript profiling during silique development demonstrates coordinated expression patterns associated with embryogenesis, seed maturation, and fruit development. Protein interaction mapping supports the quartet model, highlighting the importance of multimeric complexes in floral organ specification. Functional analyses of B-sister genes confirm their conserved roles in ovule and seed development, particularly in endothelium differentiation. Additionally, transcriptional networks controlled by AGAMOUS reveal feedback regulation and direct target gene activation during floral organogenesis. Advances in chromatin immunoprecipitation and protein tagging approaches have enabled in vivo identification of target genes. Overall, MADS-box transcription factors act as key integrators of gene regulatory networks, coordinating plant developmental processes. This review uniquely integrates molecular, genomic, and regulatory network perspectives of MADS-box transcription factors and highlights emerging research gaps and applications in crop improvement.

Keywords MADS-box genes; *Arabidopsis thaliana*; Transcription factors; CArG-box; Gene regulation; Floral development; Protein-protein interactions; Gene regulatory networks; Chromatin immunoprecipitation (ChIP); Plant development

1 Introduction

Transcriptional regulation is a key mechanism governing plant growth and development, mediated by transcription factors that bind specific cis-regulatory elements in target genes. Among these, the MADS-box transcription factor family represents one of the most important regulators of plant developmental processes, particularly in reproductive organ formation (Riechmann and Meyerowitz, 1997; Theissen et al., 2000). In *Arabidopsis thaliana*, MADS-box genes control diverse processes including floral transition, organ identity determination, ovule development, and fruit formation, highlighting their central role in plant developmental biology (Ng and Yanofsky, 2001; Ferrario et al., 2004).

MADS-domain proteins regulate gene expression through binding to conserved CArG-box cis-elements with the consensus sequence CC(A/T)$_6$ GG. However, DNA-binding specificity is not solely determined by this motif but is influenced by combinatorial interactions among transcription factors, their spatial and temporal expression patterns, and chromatin context (Shore and Sharrocks, 1995; Kaufmann et al., 2005). Despite possessing a conserved DNA-binding domain, different MADS-box proteins regulate distinct target genes, while multiple factors may act on the same regulatory regions, reflecting complex transcriptional control (de Folter and Angenent, 2006). These regulatory mechanisms are summarised in Figure 1. Importantly, these regulatory layers do not function independently. DNA-binding specificity emerges from the coordinated interplay between chromatin accessibility, higher-order MADS-box protein complex formation, cofactor recruitment, and developmental context. This integrative regulatory framework helps explain how closely related transcription factors achieve distinct developmental outputs despite recognizing similar CArG-box motifs. Furthermore, comparative studies increasingly suggest that while core regulatory principles are conserved across angiosperms, species-specific diversification of interaction networks contributes to developmental innovation in crop plants.

Genome-wide analyses have identified more than 100 MADS-box genes in *Arabidopsis*, classified into type I and type II lineages, indicating significant evolutionary diversification and functional specialization. Expression profiling studies further demonstrate coordinated yet distinct patterns during key developmental stages such as embryogenesis, seed maturation, and fruit development (Alvarez-Buylla et al., 2000; Parenicová et al., 2003).

A characteristic feature of MADS-box proteins is their ability to form dimers and higher-order complexes, which enhance regulatory specificity. These interactions underpin the “quartet model,” where multimeric protein complexes bind to multiple cis-elements to regulate floral organ identity (Egea-Cortines et al., 1999; Theissen and Saedler, 2001). Such combinatorial control mechanisms significantly expand the functional diversity of the MADS-box family (Honma and Goto, 2001; Jack, 2001). The molecular framework underlying these interactions is illustrated in Figure 1.

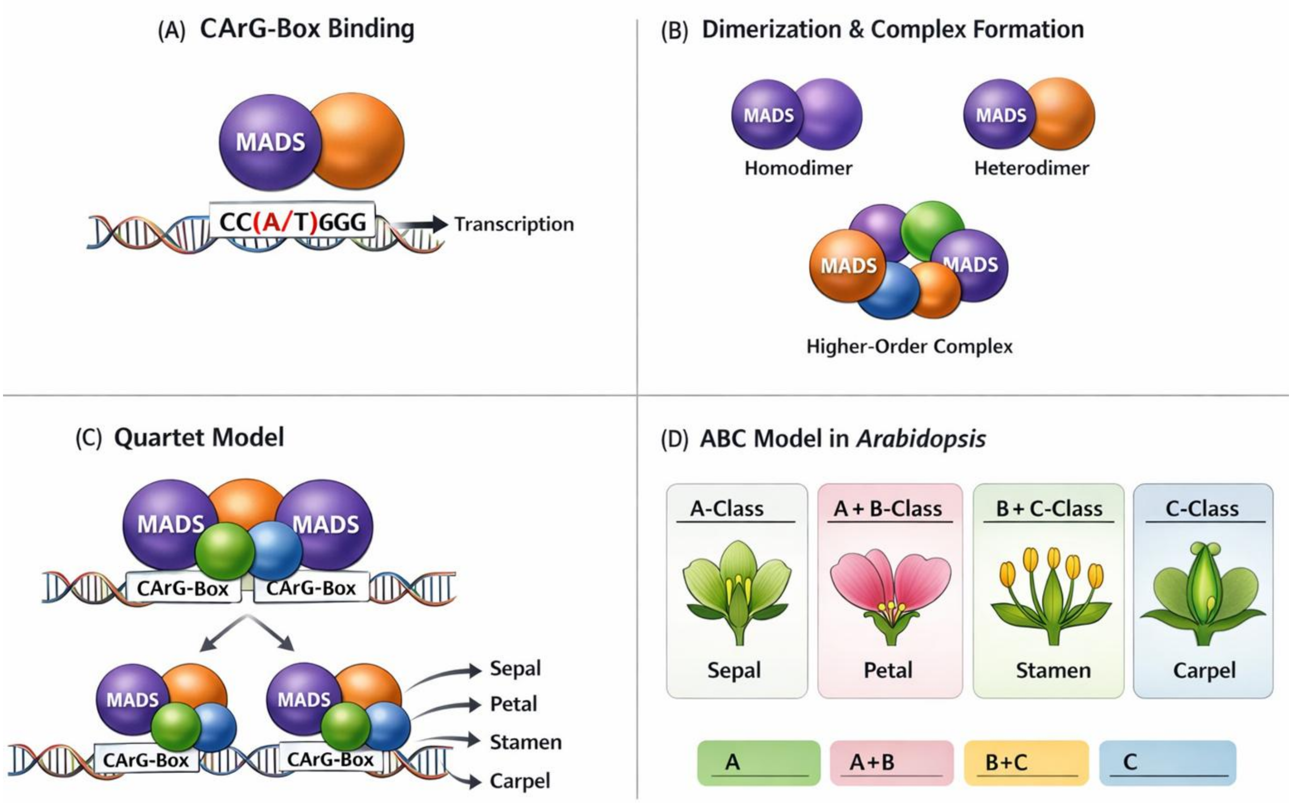

Figure 1 Regulatory framework of MADS-box transcription factors in plant development

Note: (A) MADS-box transcription factors bind to conserved CArG-box cis-regulatory elements [CC(A/T)$_6$GG] located in the promoter regions of target genes, initiating transcriptional regulation of downstream developmental processes. (B) MADS-box proteins undergo homo- and heterodimerization and can assemble into higher-order multimeric complexes, which enhance DNA-binding specificity and enable combinatorial control of gene expression. (C) Quartet model of floral organ specification, illustrating tetrameric complexes of MADS-box proteins binding to two adjacent CArG-box elements to regulate target genes involved in the determination of floral organ identity, including sepals, petals, stamens, and carpels. (D) ABC model of floral organ identity in *Arabidopsis thaliana*, showing that A-class genes specify sepals, A- and B-class genes specify petals, B- and C-class genes specify stamens, and C-class genes specify carpels

Functional studies have demonstrated that specific MADS-box genes, such as B-sister genes and AGAMOUS, play crucial roles in ovule, seed, and floral organ development through transcriptional regulation and feedback loops (Ito et al., 2004; Gómez-Mena et al., 2005). Additionally, advances in techniques such as chromatin immunoprecipitation and transcriptomic analyses have enabled the identification of direct target genes and regulatory networks (Wang et al., 2002; Taverner et al., 2004). Recent studies have further expanded our understanding of MADS-box transcription factors, highlighting their roles in complex gene regulatory networks and evolutionary diversification (Smaczniak et al., 2012; Chen et al., 2018).

Overall, MADS-box transcription factors act as central integrators of gene regulatory networks in plants. Understanding their molecular mechanisms and regulatory interactions is essential for elucidating plant developmental processes and improving crop traits. Although numerous studies have characterized MADS-box transcription factors in *Arabidopsis thaliana*, existing reviews primarily focus on either molecular function or evolutionary aspects in isolation. This review provides an integrative perspective by linking functional genomics, transcriptional regulatory networks, and epigenetic regulation, while also highlighting their translational potential in crop improvement. Furthermore, this review identifies key knowledge gaps in understanding target specificity, chromatin context dependency, and higher-order complex formation, thereby providing directions for future research.

2 Classification of MADS-box Genes

MADS-box transcription factors in plants are broadly classified into two major lineages: Type I and Type II, based on phylogenetic relationships and structural features. Type I MADS-box genes are further subdivided into Mα, Mβ, and Mγ groups, and are primarily associated with roles in gametophyte and seed development. These genes generally lack conserved protein-protein interaction domains and exhibit relatively simple gene structures. In contrast, Type II MADS-box genes, also known as MIKC-type proteins, are characterized by a modular domain structure consisting of the MADS (M), Intervening (I), Keratin-like (K), and C-terminal (C) domains. These genes are extensively involved in floral organ identity, meristem determination, and reproductive development. The MIKC-type genes are further divided into MIKC^C and MIKC* subgroups, with MIKC^C playing dominant roles in the ABC model of floral development. The structural complexity and combinatorial interaction capacity of Type II proteins underpin their functional diversification. The classification and developmental functions of major MADS-box groups are summarised in Figure 2.

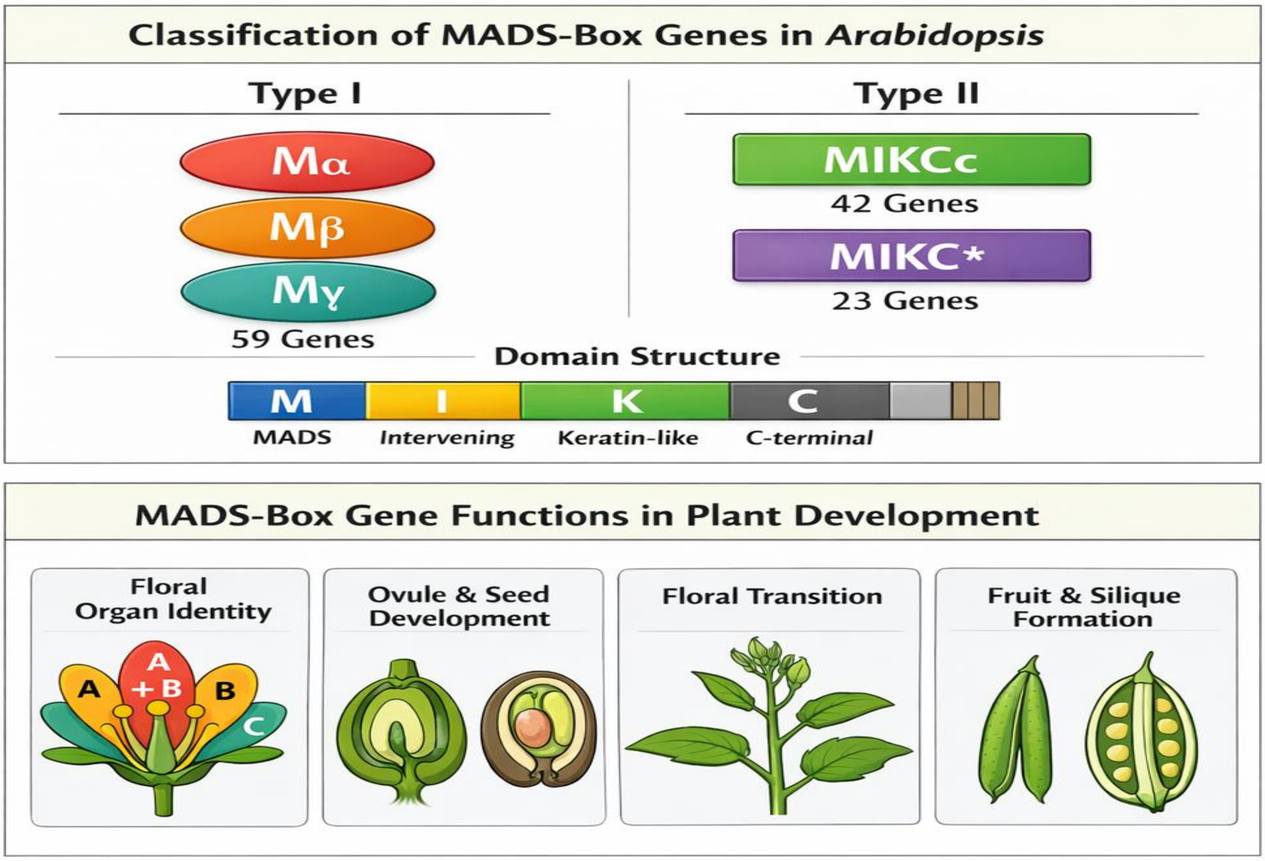

Figure 2 Classification and functions of MADS-box transcription factors in *Arabidopsis thaliana*. MADS-box genes are divided into Type I (Mα, Mβ, Mγ) and Type II (MIKC^c and MIKC*) groups. Type II proteins exhibit a conserved MIKC domain structure. These transcription factors regulate key developmental processes, including floral organ identity, ovule and seed development, floral transition, and fruit formation

2.1 Evolutionary diversification of MADS-box genes

The MADS-box gene family has undergone extensive expansion and diversification throughout plant evolution, primarily driven by gene duplication events such as whole-genome duplications and tandem duplications. Phylogenetic analyses indicate that ancestral MADS-box genes existed prior to the divergence of major eukaryotic lineages, followed by lineage-specific expansions in plants. In angiosperms, the diversification of MIKC-type genes has enabled the evolution of complex floral structures. Functional divergence following duplication has resulted in subfunctionalization and neofunctionalization, allowing paralogous genes to acquire specialized roles in distinct developmental pathways. Comparative genomics studies reveal conservation of core regulatory functions alongside species-specific innovations, highlighting the evolutionary plasticity of this gene family. Genome-wide analyses have further refined classification and functional annotation of MADS-box genes across plant species. Recent phylogenomic studies have revealed dynamic patterns of gene retention and loss, emphasizing the evolutionary plasticity of MIKC-type MADS-box genes (Gramzow and Theissen, 2015; Ruelens et al., 2017).

3 Functional Roles in Plant Development

3.1 Floral development

MADS-box transcription factors are central regulators of floral organ identity through the ABC model, where combinatorial gene activity determines the formation of sepals, petals, stamens, and carpels. Key genes such as APETALA1, PISTILLATA, and AGAMOUS coordinate organ specification via transcriptional regulation. The regulatory role of AGAMOUS and associated complexes has been further elucidated through recent molecular studies (Ó'Maoiléidigh et al., 2013). Furthermore, experimental evidence supporting the quartet model suggests that higher-order protein complexes provide an additional level of specificity. Recent evidence further suggests that quartet complex activity may depend on local chromatin accessibility and developmental stage, indicating that floral organ identity is regulated through dynamic integration of transcription factor assembly and epigenetic context rather than fixed combinatorial codes alone. However, the stability, composition, and in vivo dynamics of these complexes remain insufficiently characterized.

Importantly, discrepancies between mutant phenotypes and predicted ABC model outcomes highlight that redundancy and network buffering play significant roles in floral development. This suggests that floral organ identity is governed not by linear gene interactions, but by a robust and highly interconnected regulatory network.

3.2 Seed and ovule development

B-sister MADS-box genes have been implicated in ovule and seed coat development; however, their functional conservation across species remains only partially understood. While studies in *Arabidopsis* demonstrate a clear role in endothelium differentiation, comparative analyses suggest divergence in regulatory function in crop species.

This raises an important limitation in current research: the over-reliance on *Arabidopsis* as a model system. Although it provides valuable mechanistic insights, translating these findings to agriculturally relevant species is not straightforward due to differences in gene regulation and developmental context.

Consequently, future studies must adopt a comparative framework to determine whether observed functions represent conserved mechanisms or species-specific adaptations.

3.3 Fruit development

MADS-box genes also regulate fruit formation and ripening processes. They control tissue differentiation, cell expansion, and hormonal signalling pathways, contributing to fruit morphology and reproductive success.

3.4 Regulatory networks and epigenetic control

MADS-box transcription factors function within complex gene regulatory networks (GRNs), integrating multiple signalling pathways to control plant development. Their activity is modulated through protein-protein interactions, enabling the formation of dimers and higher-order complexes such as those described in the quartet model.

Epigenetic mechanisms further refine MADS-box gene regulation. Chromatin remodelling, histone modifications, and DNA methylation influence gene accessibility and transcriptional activity. Additionally, long non-coding RNAs and microRNAs have been implicated in post-transcriptional regulation of MADS-box genes. An important emerging concept is that transcription factor complex formation and chromatin regulation are mechanistically interconnected. MADS-box complexes may preferentially bind accessible chromatin regions, while simultaneously recruiting chromatin modifiers that reinforce transcriptional states. This reciprocal relationship likely contributes to regulatory specificity and developmental robustness. These multilayered regulatory systems ensure precise spatial and temporal gene expression during development. Advances in systems biology have enabled reconstruction of gene regulatory networks governing floral development (Chen et al., 2018). Epigenetic regulation, including chromatin modifications, plays a crucial role in modulating MADS-box gene activity. This gap highlights a broader issue in plant molecular biology: the need to move from static interaction models to dynamic, systems-level understanding. An overview of these regulatory interactions and developmental pathways is presented in Figure 3.

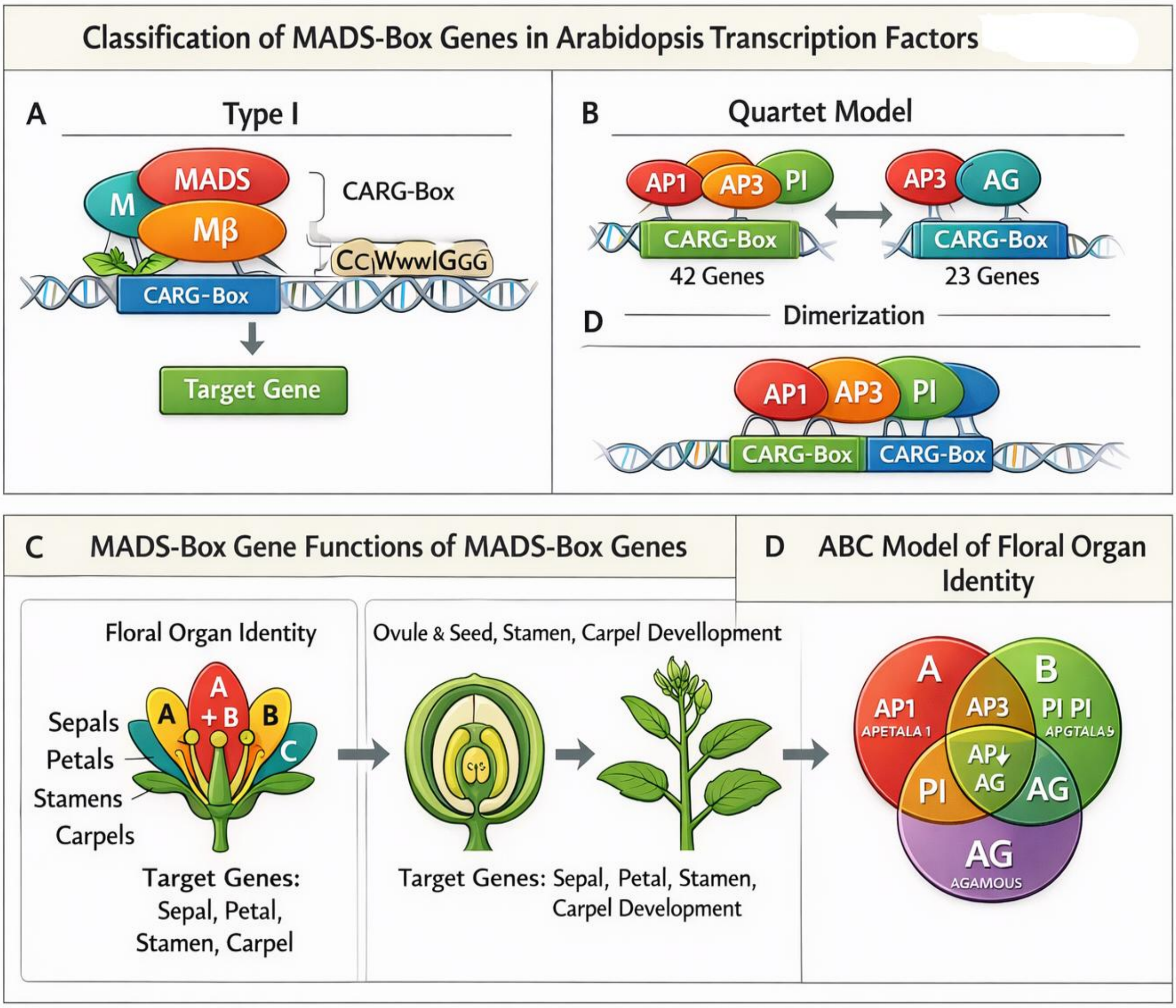

Figure 3 Regulatory roles of MADS-box transcription factors in *Arabidopsis thaliana*. MADS-box proteins bind CArG-box elements, form dimers and higher-order complexes (quartet model), and regulate floral organ identity through the ABC model, controlling key developmental processes

Importantly, these regulatory layers do not function independently but operate as an interconnected system that determines developmental specificity. The formation of distinct MADS-box transcription factor complexes influences DNA-binding selectivity, while chromatin accessibility and epigenetic modifications further determine whether target loci can be transcriptionally activated or repressed. Thus, regulatory specificity emerges from the combined effects of protein complex composition, cis-regulatory context, and chromatin state. Insights from *Arabidopsis* have therefore provided a foundational framework for understanding conserved transcriptional regulatory mechanisms in plants, with increasing relevance for translational studies aimed at improving flowering behaviour, seed development, fruit traits, and environmental adaptability in crop species.

3.5 Applications in crop improvement

Understanding MADS-box gene function has significant implications for agricultural biotechnology. Manipulation of these genes can enhance traits such as flowering time, fruit quality, seed development, and yield. For example, modification of floral regulators can optimise flowering for different climatic conditions. Targeting fruit-related MADS genes can improve ripening and shelf life. Engineering seed development pathways can increase productivity. Advances in genome editing technologies, particularly CRISPR/Cas systems, have enabled precise functional studies and targeted manipulation of MADS-box genes. These approaches provide powerful tools for developing improved crop varieties with enhanced agronomic traits.

4 Knowledge Gaps and Future Perspectives

4.1 Challenges in understanding MADS-box regulatory specificity

Despite substantial conceptual and technological advances in understanding MADS-box transcription factors in *Arabidopsis thaliana*, several fundamental mechanistic questions remain unresolved that limit a comprehensive understanding of their regulatory mechanisms and functional specificity.

One of the major unresolved questions is the specificity of CArG-box binding. Although the consensus sequence CC $(A/T)_6$ GG is well established, it is widely distributed throughout the genome, raising questions about how MADS-box proteins selectively regulate target genes. Emerging evidence suggests that binding specificity is influenced by chromatin context, cofactor interactions, and higher-order protein complex formation; however, these factors remain insufficiently characterized. Collectively, current research has firmly established that MADS-box transcription factors act through combinatorial protein interactions, higher-order complex formation, and binding to CArG-box cis-elements to regulate floral and reproductive development. It is also well supported that chromatin accessibility and epigenetic modifications influence transcriptional activity. However, major uncertainties remain regarding how these regulatory layers are integrated in vivo to achieve developmental specificity. In particular, the dynamic assembly of transcription factor complexes, the contribution of local chromatin architecture to target selection, and the extent to which these mechanisms are conserved across plant species remain incompletely understood. Emerging approaches including single-cell multi-omics, spatial transcriptomics, live-cell imaging, chromatin conformation analyses, and AI-assisted network modelling are expected to provide deeper mechanistic insights into these unresolved questions.

Another important limitation is the lack of high-resolution spatiotemporal data. Most transcriptomic studies are based on bulk tissue analysis, which obscures cell-type-specific regulatory dynamics. The application of single-cell RNA sequencing and spatial transcriptomics could provide deeper insights into the precise roles of MADS-box genes during different developmental stages, particularly in floral organogenesis and seed development.

Furthermore, while protein-protein interactions and regulatory networks have been extensively proposed, functional validation of these networks remains incomplete. Advanced genome editing technologies, such as CRISPR/Cas systems, offer powerful tools for targeted mutagenesis and gene function analysis, yet their application in systematically dissecting MADS-box regulatory circuits is still limited.

The role of epigenetic regulation and chromatin architecture also represents an emerging frontier. Although studies have highlighted the importance of histone modifications, DNA methylation, and chromatin remodelling in modulating MADS-box gene activity, the integration of these epigenetic layers with transcription factor binding and gene regulatory networks is not fully understood.

Finally, translating knowledge from *Arabidopsis* to crop species remains a significant challenge. While MADS-box genes are evolutionarily conserved, their functional divergence across species necessitates comparative and translational studies to effectively harness their potential for crop improvement.

In the future, integrative approaches combining multi-omics technologies, high-resolution imaging, genome editing, and computational modeling will be essential to unravel the complexity of MADS-box-mediated regulatory networks. A major future challenge will be integrating transcription factor occupancy, chromatin architecture, protein interaction dynamics, and developmental signalling into predictive regulatory models capable of explaining context-dependent developmental outcomes. Such efforts will not only advance fundamental plant biology but also facilitate the development of improved crop varieties with desirable agronomic traits.

5 Conclusion

MADS-box transcription factors represent a central regulatory module governing plant developmental processes, particularly those associated with reproductive organ formation. As illustrated in Figure 1, their function is based on a hierarchical and highly coordinated framework that integrates cis-trans interactions, combinatorial protein complex formation, and gene regulatory network dynamics. The binding of MADS-domain proteins to CArG-box cis-elements constitutes the primary mechanism of transcriptional control; however, specificity is further refined through dimerization and higher-order complex assembly, as demonstrated by the quartet model (Honma and Goto, 2001; Jack, 2001).

Genome-wide and phylogenetic analyses highlight the extensive diversification of the MADS-box gene family in *Arabidopsis thaliana*, enabling functional specialization across multiple developmental pathways. Transcriptomic studies further reveal coordinated and stage-specific expression patterns associated with embryogenesis, seed maturation, and fruit development. Functional characterization of key genes, including B-sister MADS-box members and AGAMOUS, underscores their critical roles in ovule, seed, and floral organ development through complex transcriptional networks and feedback regulation.

Advances in molecular techniques, such as chromatin immunoprecipitation and protein tagging, have significantly improved the identification of direct target genes and in vivo protein-DNA interactions, providing deeper insights into regulatory mechanisms. Nevertheless, the widespread occurrence of CArG-box-like sequences across the genome suggests that additional factors, including chromatin context, cofactor interactions, and protein complex composition, are essential determinants of binding specificity.

In conclusion, MADS-box transcription factors act as key integrators of plant gene regulatory networks, coordinating developmental signalling through dynamic and multi-layered regulatory mechanisms. Future research focusing on high-resolution mapping of transcriptional networks, identification of cofactors, and real-time analysis of protein-DNA interactions will be critical to fully elucidate the complexity and specificity of MADS-mediated regulation. Such insights will not only advance fundamental plant biology but also provide opportunities for targeted manipulation of traits relevant to crop improvement. Importantly, this review bridges the gap between molecular mechanisms and systems-level regulatory networks of MADS-box transcription factors, emphasising the need for integrative approaches combining genomics, epigenetics, and functional validation. Such a framework is essential for translating fundamental insights from *Arabidopsis* into crop improvement strategies.

Acknowledgements

The author acknowledges the contributions of researchers and collaborators whose work on MADS-box transcription factors has significantly advanced understanding of plant developmental biology. Insights synthesised in this review are based on studies conducted at Plant Research International, Wageningen-UR, and benefited from the scientific guidance and support of colleagues and collaborators in the field. The author extends appreciation to Prof. Gerco C. Angenent for his contributions to MADS-box research and to all researchers whose experimental and conceptual work formed the basis of this review.

Conflict of Interest Disclosure

The author declares that there are no conflicts of interest regarding the publication of this review paper. The author confirms that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Alvarez-Buylla E.R., Pelaz S., Liljegren S.J., Gold S.E., Burgeff C., Ditta G.S., Ribas de Pouplana L., Martínez-Castilla L., and Yanofsky M.F., 2000, An ancestral MADS-box gene duplication occurred before the divergence of plants and animals, Proceedings of the National Academy of Sciences, 97(10): 5328-5333.
https://doi.org/10.1073/pnas.97.10.5328

Chen D., Yan W., Fu L.Y., and Kaufmann K., 2018, Architecture of gene regulatory networks controlling flower development in *Arabidopsis thaliana*, Nature Communications, 9(1): 4534.
https://doi.org/10.1038/s41467-018-06772-3

de Folter S., and Angenent G.C., 2006, Trans meets cis in MADS science, Trends in Plant Science, 11(5): 224-231.
https://doi.org/10.1016/j.tplants.2006.03.008

Egea-Cortines M., Saedler H., and Sommer H., 1999, Ternary complex formation between the MADS-box proteins SQUAMOSA, DEFICIENS and GLOBOSA is involved in the control of floral architecture in Antirrhinum majus, The EMBO Journal, 18(19): 5370-5379.
https://doi.org/10.1093/emboj/18.19.5370

Ferrario S., Immink R.G., and Angenent G.C., 2004, Conservation and diversity in flower land, Current Opinion in Plant Biology, 7(1): 84-91.
https://doi.org/10.1016/j.pbi.2003.11.003

Gómez-Mena C., de Folter S., Costa M.M.R., Angenent G.C., and Sablowski R., 2005, Transcriptional program controlled by the floral homeotic gene AGAMOUS during early organogenesis, Development, 132(3): 429-438.
https://doi.org/10.1242/dev.01600

Gramzow L., and Theissen G., 2015, Phylogenomics reveals surprising sets of essential and dispensable clades of MIKCc-group MADS-box genes in flowering plants, Journal of Experimental Zoology Part B: Molecular and Developmental Evolution, 324(4): 353-362.
https://doi.org/10.1002/jez.b.22598

Honma T., and Goto K., 2001, Complexes of MADS-box proteins are sufficient to convert leaves into floral organs, Nature, 409(6819): 525-529.
https://doi.org/10.1038/35054083

Ito T., Wellmer F., Yu H., Das P., Ito N., Alves-Ferreira M., Riechmann J.L., and Meyerowitz E.M., 2004, The homeotic protein AGAMOUS controls microsporogenesis by regulation of SPOROCYTELESS, Nature, 430(6997): 356-360.
https://doi.org/10.1038/nature02733

Jack T., 2001, Relearning our ABCs: new twists on an old model, Trends in Plant Science, 6(7): 310-316.
https://doi.org/10.1016/S1360-1385(01)01987-2

Kaufmann K., Melzer R., and Theissen G., 2005, MIKC-type MADS-domain proteins: structural modularity, protein interactions and network evolution in land plants, Gene, 347(2): 183-198.
https://doi.org/10.1016/j.gene.2004.12.014

Ng M., and Yanofsky M.F., 2001, Function and evolution of the plant MADS-box gene family, Nature Reviews Genetics, 2(3): 186-195.
https://doi.org/10.1038/35056041

Ó'Maoiléidigh D.S., Wuest S.E., Rae L., Raganelli A., Ryan P.T., Kwaśniewska K., Das P., Lohan A.J., Loftus B., Graciet E., and Wellmer F., 2013, Control of reproductive floral organ identity specification in *Arabidopsis* by the C function regulator AGAMOUS, The Plant Cell, 25(7): 2482-2503.
https://doi.org/10.1105/tpc.113.113209

Parenicová L., De Folter S., Kieffer M., Horner D.S., Favalli C., Busscher J., Cook H.E., Ingram R.M., Kater M.M., Davies B., Angenent G.C., and Colombo L., 2003, Molecular and phylogenetic analyses of the complete MADS-box transcription factor family in *Arabidopsis*: new openings to the MADS world, The Plant Cell, 15(7): 1538-1551.
https://doi.org/10.1105/tpc.011544

Riechmann J.L., and Meyerowitz E.M., 1997, MADS domain proteins in plant development, Biological Chemistry, 378(10): 1079-1101.

Ruelens P., Zhang Z., Van Mourik H., Maere S., Kaufmann K., and Geuten K., 2017, The origin of floral organ identity quartets, The Plant Cell, 29(2): 229-242.
https://doi.org/10.1105/tpc.16.00366

Shore P., and Sharrocks A.D., 1995, The MADS-box family of transcription factors, European Journal of Biochemistry, 229(1): 1-13.
https://doi.org/10.1111/j.1432-1033.1995.tb20430.x

Smaczniak C., Immink R.G., Angenent G.C., and Kaufmann K., 2012, Developmental and evolutionary diversity of plant MADS-domain factors: insights from recent studies, Development, 139(17): 3081-3098.
https://doi.org/10.1242/dev.074674

Taverner N.V., Smith J.C., and Wardle F.C., 2004, Identifying transcriptional targets, Genome Biology, 5(3): 210.
https://doi.org/10.1186/gb-2004-5-3-210

Theissen G., and Saedler H., 2001, Floral quartets, Nature, 409(6819): 469-471.
https://doi.org/10.1038/35054172

Theissen G., Becker A., Di Rosa A., Kanno A., Kim J.T., Münster T., Winter K., and Saedler H., 2000, A short history of MADS-box genes in plants, Plant Molecular Biology, 42(1): 115-149.
https://doi.org/10.1023/A:1006332105728

Wang H., Tang W., Zhu C., and Perry S.E., 2002, A chromatin immunoprecipitation (ChIP) approach to isolate genes regulated by AGL15, a MADS domain protein that preferentially accumulates in embryos, The Plant Journal, 32(5): 831-843. https://doi.org/10.1046/j.1365-313X.2002.01455.x