

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.

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