

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  $M\alpha$ ,  $M\beta$ , and  $M\gamma$  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.

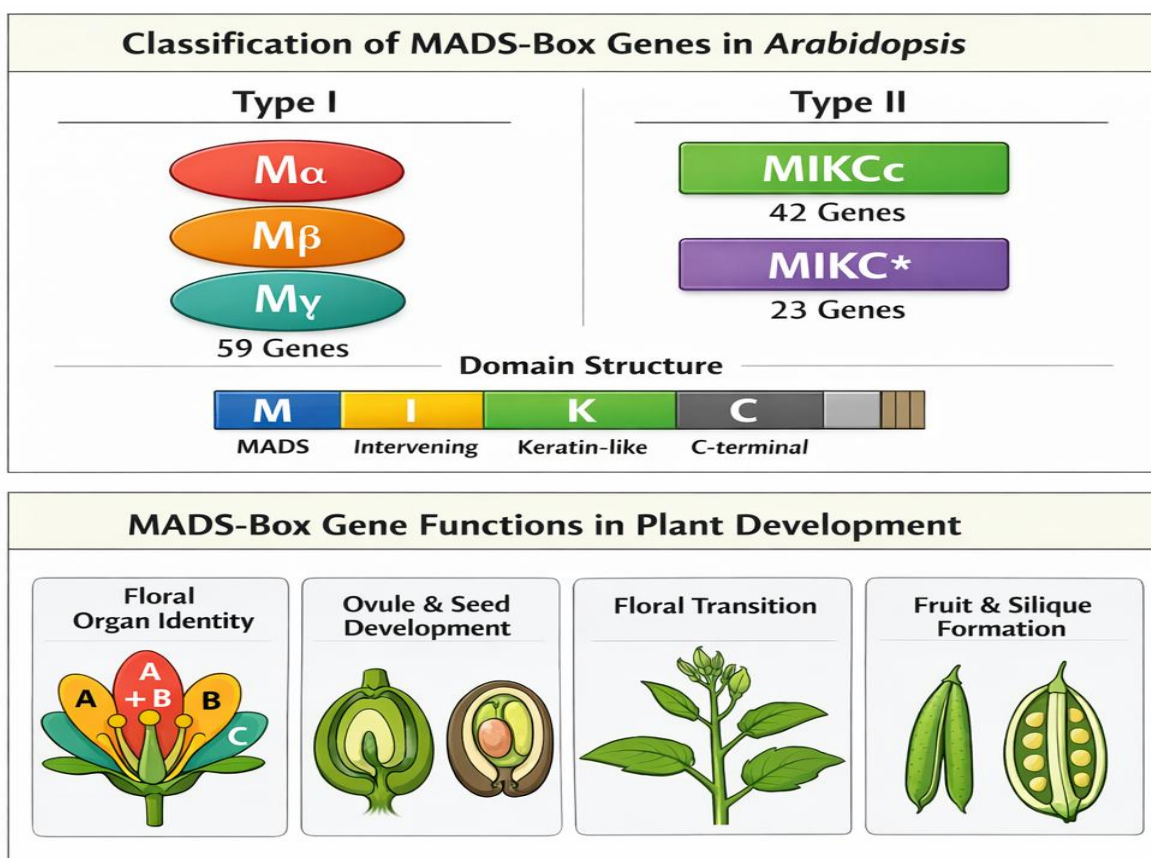


Figure 2 Classification and functions of MADS-box transcription factors in *Arabidopsis thaliana*. MADS-box genes are divided into Type I ( $M\alpha$ ,  $M\beta$ ,  $M\gamma$ ) and Type II ( $MIKC^C$  and  $MIKC^*$ ) groups. Type II proteins exhibit a conserved MIKC domain structure. These transcription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