

ANY MERISTEM (BAM1/2), and RECEPTOR-LIKE PROTEIN KINASE2 (RPK2), which coordinate cell fate determination and tissue patterning (DeYoung et al., 2006; Hord et al., 2006; Mizuno et al., 2007; Cui et al., 2018; Hu et al., 2018).

Further progression of anther development involves the formation of distinct somatic layers, including the epidermis, endothecium, middle layer, and tapetum, surrounding the microspore mother cells. Key regulators such as SPOROCTELESS/NOZZLE (SPL/NZZ) play a pivotal role in initiating sporogenesis (Schiefthaler et al., 1999; Yang et al., 1999; Ito et al., 2004), while signaling pathways involving EMS1–TPD1 and MAP kinases (MPK3 and MPK6) govern tapetum differentiation and function (Canales et al., 2002; Zhao et al., 2002; Yang et al., 2003; Jia et al., 2008; Zhao et al., 2017). The tapetum, in particular, is crucial for providing nutrients and materials required for pollen wall formation, and its proper development is essential for viable pollen production (Kapoor et al., 2002; Zheng et al., 2003; Zhang et al., 2006; Zhang and Yang, 2014).

In addition to genetic regulation, hormonal signaling pathways significantly influence stamen development. Phytohormones such as jasmonic acid (Feys et al., 1994; McConn and Browse, 1996; Sanders et al., 2000; Stintzi and Browse, 2000; Ishiguro et al., 2001; Ito et al., 2007), gibberellins (Cheng et al., 2004; Fleet and Sun, 2005; Hou et al., 2008; Iuchi et al., 2007), and auxins (Nagpal et al., 2005; Cecchetti et al., 2008) coordinate critical processes including filament elongation, pollen maturation, and anther dehiscence. The interplay between these hormonal pathways ensures the temporal synchronization of reproductive events necessary for successful pollination.

Comparative studies in other angiosperms, including genera such as *Salvia* and *Gerbera* (Kramer and Irish, 1999; Kotilainen et al., 2000; Kramer and Irish, 2000; Wetters, 2020), have revealed both conserved and divergent roles of floral regulatory genes, particularly MADS-box genes, in stamen development. These studies highlight the evolutionary conservation of core regulatory networks alongside species-specific adaptations that contribute to floral diversity.

Overall, stamen development is governed by a complex interplay of genetic, molecular, and hormonal factors. Understanding these regulatory networks not only provides insights into fundamental plant developmental biology but also has important implications for crop improvement, hybrid seed production, and fertility regulation.

Recent advances in plant molecular biology have substantially improved our understanding of the regulatory mechanisms governing stamen development. High-throughput multi-omics approaches, including transcriptomics, proteomics, and epigenomics, have enabled comprehensive identification of genes, proteins, and regulatory pathways involved in anther development and pollen formation. In particular, single-cell RNA sequencing (scRNA-seq) has provided unprecedented resolution of cell-type-specific gene expression during anther ontogeny, revealing dynamic regulatory networks underlying tapetum differentiation and microsporogenesis. Furthermore, CRISPR/Cas-mediated genome editing has emerged as a powerful tool for functional validation of candidate genes such as SPL/NZZ, EMS1, BAM1/BAM2, RPK2, and MADS-box transcription factors, facilitating precise investigation of their roles in reproductive development. Integration of these advanced genomic technologies with classical genetic studies is expected to accelerate the discovery of novel regulatory mechanisms and support future applications in crop improvement, hybrid breeding, and fertility regulation.

2 Results

2.1 Stamen specification through ABC model genes

Previous studies have demonstrated that floral organ identity is governed by the combinatorial activity of B-, C-, and E-class genes. The coordinated expression of APETALA3 (AP3), PISTILLATA (PI), and AGAMOUS (AG) is essential for proper stamen specification. Genetic studies have shown that disruption of these genes results in the loss or homeotic transformation of stamens, highlighting their critical role in reproductive organ identity and development (Figure 1) (Bowman et al., 1989; 1991; Coen and Meyerowitz, 1991; Pelaz et al., 2000).