

anther cell fate determination. Previous studies have reported that mutations in these genes result in defective archesporial cell division and improper specification of parietal layers. Higher-order mutants lacking CIKs and RPK2 exhibit severe developmental defects, including the absence of somatic cell layers and overproduction of sporogenous cells, suggesting that these kinases function within a common signaling pathway (Albrecht et al., 2005; Colcombet et al., 2005; Hord et al., 2006; Mizuno et al., 2007; Cui et al., 2018; Hu et al., 2018).

2.4 Regulation of sporogenesis and tapetum development

Previous studies have demonstrated that SPOROCTELESS/NOZZLE (SPL/NZZ) is indispensable for the initiation of sporogenesis (Yang et al., 1999; Schiefthaler et al., 1999; Ito et al., 2004). Loss-of-function mutants fail to produce microsporogenous cells and tapetal tissues. In addition, the EMS1–TPD1 signaling pathway together with MAP kinases (MPK3/MPK6) plays a crucial role in tapetum differentiation and function (Canales et al., 2002; Zhao et al., 2002; Yang et al., 2003; Jia et al., 2008; Zhao et al., 2017). Disruption of these pathways results in abnormal tapetal development and impaired pollen formation.

2.5 Genetic control of anther morphogenesis

Previous studies have demonstrated that JAGGED (JAG) and NUBBIN (NUB) regulate the growth and structural organization of microsporangia. Mutant analyses indicate that these genes primarily promote tissue growth rather than floral organ identity specification.

2.6 Hormonal regulation of stamen development

Several studies have shown that jasmonic acid, gibberellins, and auxins play crucial roles in coordinating the later stages of stamen development. Jasmonic acid is required for pollen maturation and anther dehiscence, whereas gibberellins promote filament elongation. Auxin regulates the timing of pollen release and prevents premature anther dehiscence (Yang et al., 2007). Mutants deficient in these hormonal pathways frequently exhibit male sterility (Mandaokar et al., 2006) or delayed reproductive development (Feys et al., 1994; Ishiguro et al., 2001; Cheng et al., 2004; Cecchetti et al., 2008).

2.7 Comparative insights from other angiosperms

Comparative studies across angiosperms have demonstrated conserved expression patterns of B- and C-class MADS-box genes in stamen tissues. However, species-specific differences in gene expression dynamics and regulatory mechanisms have also been reported. In *Gerbera*, the GRCD1 gene plays a critical role in stamen identity, and its downregulation results in the homeotic transformation of stamens into petal-like structures. These findings highlight both the evolutionary conservation and diversification of floral developmental regulatory networks.

2.8 Integration of regulatory networks

Collectively, previous studies indicate that stamen development is regulated by an integrated network of genetic regulators, receptor-mediated signaling pathways, and phytohormonal cues. These components interact in a coordinated manner to regulate cell division, tissue differentiation, tapetum development, microsporogenesis, pollen maturation, and anther dehiscence, thereby ensuring successful male reproductive development in flowering plants (Figure 2).

3 Discussion

Stamen development represents a highly coordinated developmental program integrating genetic, molecular, and hormonal controls. The present synthesis highlights that the ABC (ABCDE) model remains a central framework for understanding floral organ identity, with B-, C-, and E-class MADS-box genes (*APETALA3*, *PISTILLATA*, and *AGAMOUS*) functioning as key determinants of stamen specification (Coen and Meyerowitz, 1991; Pelaz et al., 2000; Alvarez-Buylla et al., 2010). The conservation of this regulatory module across angiosperms underscores its evolutionary significance, while variations observed in other species indicate adaptive diversification of floral structures.