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Molecular Genetic Regulation of Stamen Development: Insights from the ABC Model and Anther Ontogeny in *Arabidopsis* and Other Angiosperms

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

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Abstract Stamen development is a critical process governing male fertility in flowering plants and is tightly regulated by genetic and hormonal networks. The ABC model of floral organ identity, extended to include D and E functions, explains stamen specification through the combined activity of B-, C-, and E-class MADS-box genes such as *APETALA3*, *PISTILLATA*, and *AGAMOUS*. In *Arabidopsis thaliana*, anther development proceeds through fourteen stages involving coordinated cell division, differentiation, and tissue organization. Early developmental events are controlled by receptor-like kinases including CIKs, BAM1/2, and RPK2, which regulate archesporial cell fate and parietal layer formation. Additional regulators such as SPL/NZZ, EMS1–TPD1 signaling, and MAP kinases contribute to microsporogenesis and tapetum function. Hormonal pathways involving jasmonates, gibberellins, and auxins further coordinate pollen maturation and anther dehiscence. Comparative studies in other angiosperms reveal both conserved and species-specific regulatory mechanisms.

Keywords Stamen development; ABC model; MADS-box genes; *Arabidopsis thaliana*; Anther development; Microsporogenesis; Tapetum; Hormonal regulation

1 Introduction

Flowering plants (angiosperms) possess highly specialized reproductive structures, with the flower representing one of the most complex organs in plant development. A typical hermaphroditic flower is organized into concentric whorls consisting of sepals, petals, stamens, and carpels, each arising from a determinate floral meristem. Among these, the stamen constitutes the male reproductive organ and plays a central role in pollen production and successful fertilization. Structurally, a stamen comprises a filament that supports the anther, where pollen grains are formed within specialized compartments known as microsporangia. Proper development of stamens is therefore essential for plant fertility and reproductive success.

The genetic basis of floral organ identity has been extensively explained by the ABC model, later expanded into the ABCDE model, which describes how combinations of MADS-box transcription factors specify distinct floral organs (Schwarz-Sommer et al., 1990). In this framework, stamens are specified by the combined action of B-, C-, and E-class genes, including *APETALA3 (AP3)*, *PISTILLATA (PI)*, and *AGAMOUS (AG)* (Bowman et al., 1991; Pelaz et al., 2000; Ng and Yanofsky, 2001; Becker and Theißen, 2003). These genes regulate downstream targets that control organ identity as well as the initiation and differentiation of reproductive tissues (Shore and Sharrocks, 1995; Riechmann and Meyerowitz, 1997). Mutations in these regulatory genes often result in homeotic transformations, highlighting their fundamental role in floral patterning (Bowman et al., 1989; 1991; Coen and Meyerowitz, 1991; Pelaz et al., 2000; Pinyopich et al., 2003; Alvarez-Buylla et al., 2010).

The model plant *Arabidopsis thaliana* has provided critical insights into the molecular and cellular mechanisms underlying stamen and anther development (Ma, 2005; Bowman, 2012). Anther ontogeny in *Arabidopsis* is divided into fourteen distinct stages characterized by precise patterns of cell division, differentiation, and tissue organization (Owen and Makaroff, 1995; Sanders et al., 1999). Early developmental events involve the specification of archesporial cells and their differentiation into sporogenous and somatic cell lineages. This process is tightly regulated by receptor-like kinases such as CLAVATA3 INSENSITIVE RECEPTOR KINASEs (CIKs), BARELY

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 SPOROCYTELESS/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).

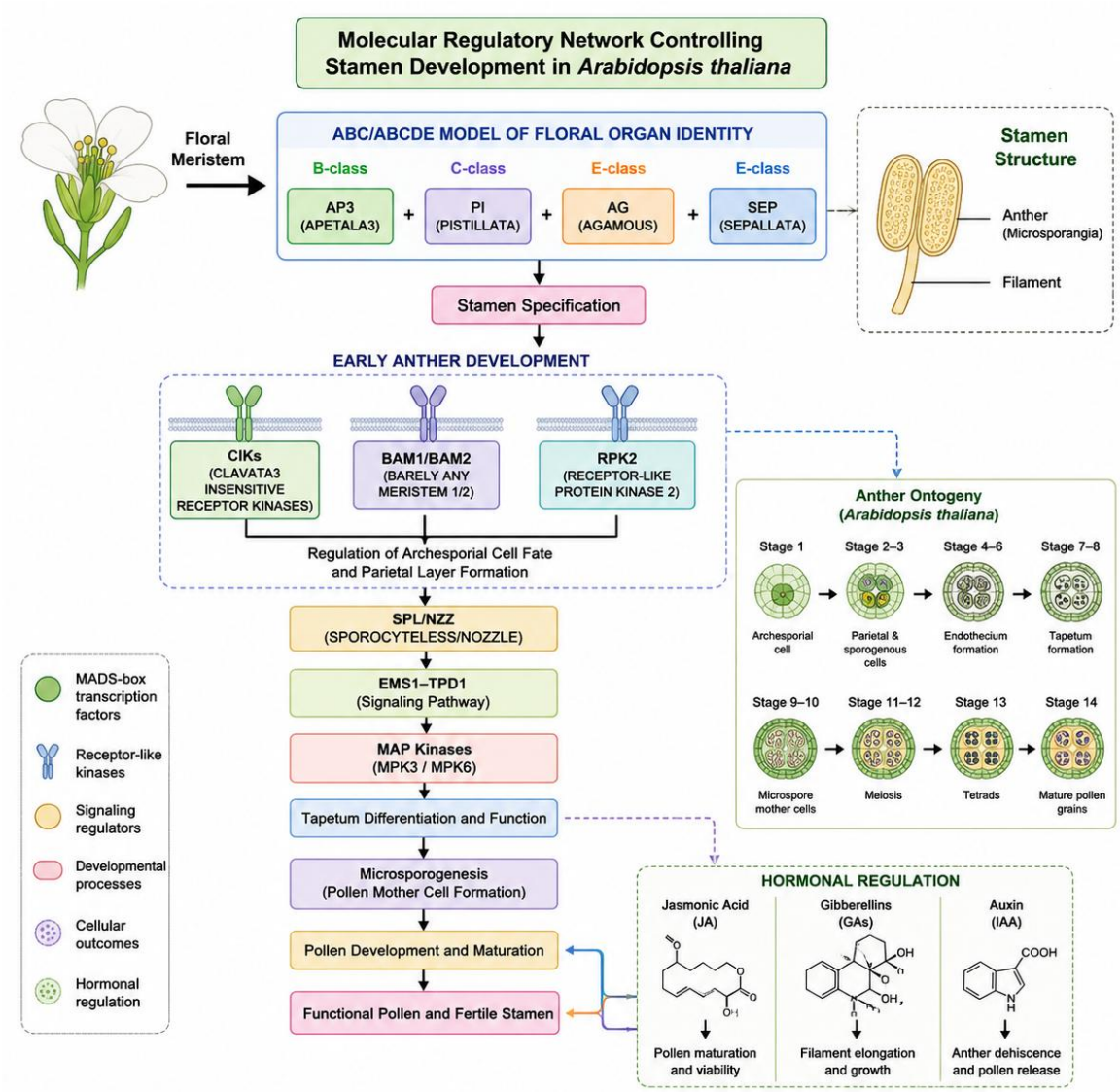

Figure 1 Molecular regulatory network controlling stamen development in *Arabidopsis thaliana*

Image caption: Floral organ identity is established through the coordinated activities of the ABC/ABCDE floral homeotic genes, including APETALA3 (AP3), PISTILLATA (PI), AGAMOUS (AG), and SEPALLATA (SEP). Early anther development is regulated by receptor-like kinases (CIKs, BAM1/BAM2, and RPK2) that control archesporial cell specification and anther patterning. Subsequent activation of the SPL/NZZ, EMS1–TPD1, and MAPK (MPK3/MPK6) signaling pathways promotes tapetum differentiation and microsporogenesis. Plant hormones, including jasmonic acid (JA), gibberellins (GAs), and auxin (IAA), regulate pollen maturation, filament elongation, and anther dehiscence, ultimately leading to the formation of functional pollen and male fertility. The diagram summarizes the major molecular and hormonal regulatory pathways described in this review

2.2 Stages of anther development in *Arabidopsis thaliana*

Previous developmental studies have shown that anther development in *Arabidopsis thaliana* proceeds through fourteen distinct stages characterized by sequential cellular and morphological changes. Early stages (1~5) involve the formation of anther primordia and differentiation of archesporial cells into primary sporogenous and parietal cells. Intermediate stages (6~8) are characterized by meiosis of microspore mother cells and tetrad formation, followed by release of microspores. Late stages (9~14) include pollen maturation and anther dehiscence, completing the reproductive process (Owen and Makaroff, 1995; Sanders et al., 1999; Ma, 2005).

2.3 Role of receptor-like kinases in early anther development

Accumulated evidence indicates that CLAVATA3 INSENSITIVE RECEPTOR KINASEs (CIKs), BARELY ANY MERISTEM (BAM1/BAM2), and RECEPTOR-LIKE PROTEIN KINASE2 (RPK2) play essential roles in early

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 SPOROCYTELESS/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.

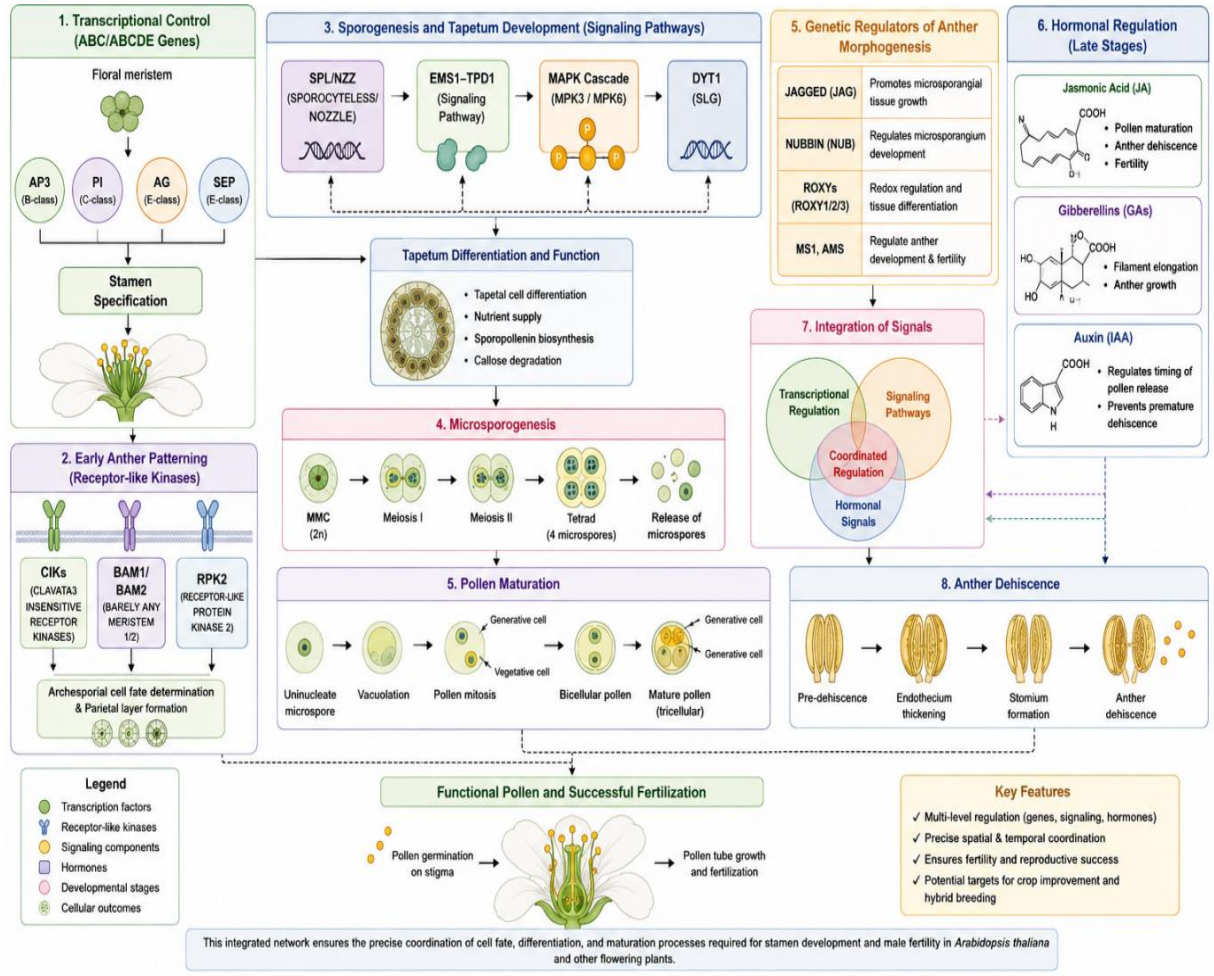

Figure 2 Integrated regulatory network governing anther development, pollen maturation, and male fertility in flowering plants

Image caption: The figure illustrates the coordinated regulation of male reproductive development by transcription factors, receptor-like kinases, signaling pathways, and phytohormones. Early anther patterning is regulated by *CIKs, BAM1/BAM2,* and *RPK2*, followed by activation of *SPL/NZZ*, *EMS1–TPD1*, MAP kinase signaling, and additional regulators controlling tapetum differentiation and microsporogenesis. Hormonal pathways involving jasmonic acid, gibberellins, and auxin regulate pollen maturation, filament elongation, and anther dehiscence. The integration of these molecular networks ensures successful pollen development, fertilization, and male fertility, providing potential targets for functional genomics, hybrid breeding, genome editing, and crop improvement

The staged progression of anther development in *Arabidopsis thaliana* provides a valuable model for dissecting the cellular and molecular mechanisms underlying male reproductive development. Early events, particularly archesporial cell specification and parietal layer formation, are tightly regulated by receptor-like kinases such as CIKs, BAM1/2, and RPK2 (Hord et al., 2006; Mizuno et al., 2007; Cui et al., 2018). The phenotypic similarities observed in higher-order mutants suggest that these kinases operate within interconnected signaling pathways to maintain stem cell homeostasis and ensure proper tissue differentiation (Albrecht et al., 2005; Hu et al., 2018). Their interaction and phosphorylation dynamics further emphasize the importance of signal transduction in early anther patterning.

Transcriptional regulators such as SPOROCYTELESS/NOZZLE (SPL/NZZ) play a pivotal role in initiating sporogenesis, acting downstream of floral identity genes (Yang et al., 1999; Ito et al., 2004). In parallel, the EMS1–TPD1 signaling module and MAP kinase pathways (MPK3/MPK6) are essential for tapetum differentiation and function (Jia et al., 2008; Zhao et al., 2017). The tapetum emerges as a critical tissue, not only supporting pollen development but also influencing fertility outcomes, as evidenced by numerous mutants exhibiting male sterility due to tapetal defects (Zhang et al., 2006; Zhang and Yang, 2014). These findings reinforce the concept that successful microsporogenesis depends on precise coordination between sporogenous and somatic tissues.

Genes such as JAGGED (JAG) and NUBBIN (NUB) contribute to anther morphogenesis by promoting microsporangial growth rather than identity specification, indicating the existence of parallel regulatory pathways governing structural development.

Hormonal regulation adds another layer of complexity to stamen development. Jasmonic acid, gibberellins, and auxins act in a coordinated manner to regulate filament elongation, pollen maturation, and anther dehiscence. The crosstalk between these hormones ensures temporal synchronization of developmental events, which is crucial for successful fertilization. Mutant analyses further confirm that disruption in hormonal balance leads to defects in fertility, emphasizing their integrative role (Ishiguro et al., 2001; Cheng et al., 2004; Cecchetti et al., 2008).

These comparative studies indicate that the core molecular mechanisms governing stamen development have been largely conserved during angiosperm evolution. Nevertheless, lineage-specific modifications in gene expression patterns, regulatory interactions, and duplication of MADS-box genes have contributed to the remarkable diversity of floral morphology and reproductive strategies observed among flowering plants. Future comparative genomic and evolutionary developmental (evo-devo) studies will further clarify the origin and diversification of these regulatory networks.

Beyond its fundamental biological significance, understanding the molecular regulation of stamen development has important applications in modern crop improvement and sustainable agriculture. Genes regulating tapetum differentiation and anther development, including *SPL/NZZ*, *EMS1–TPD1*, *BAM1/BAM2*, and *DYT1*, have been widely investigated for the development of stable genetic male-sterility systems used in hybrid seed production (Mariani et al., 1990; Mariani et al., 1991; Denis et al., 1993). Recent advances in CRISPR/Cas-mediated genome editing have further enabled precise manipulation of floral regulatory genes for fertility control, functional validation, and de novo crop domestication. In addition, hormone-regulated pathways involving jasmonic acid, auxin, and gibberellins provide promising targets for improving pollen fertility and reproductive performance under abiotic stresses such as heat and drought. Comparative studies across diverse crop species are expected to accelerate molecular breeding strategies for the development of climate-resilient cultivars with enhanced reproductive efficiency. Furthermore, the integration of multi-omics technologies, including transcriptomics, proteomics, metabolomics, and single-cell sequencing, will facilitate the identification of novel regulatory genes and signaling networks controlling male reproductive development. These advances will not only improve our understanding of the molecular basis of stamen development but also support the development of next-generation crop varieties with enhanced yield, reproductive stability, and resilience under changing climatic conditions. Moreover, integrating artificial intelligence-assisted data analysis with functional genomics and genome editing is expected to accelerate the discovery of novel regulatory genes and improve predictive breeding strategies. Such interdisciplinary approaches will enhance the translation of fundamental knowledge into practical applications for sustainable agriculture and global food security.

4 Conclusion

Stamen development is a complex and tightly regulated process essential for plant reproduction, controlled by the coordinated action of floral identity genes, signaling pathways, and hormonal networks. The ABCDE model provides a robust framework for understanding stamen specification, while studies in *Arabidopsis thaliana* and other species have revealed intricate mechanisms governing anther development, microsporogenesis, and pollen maturation. Key regulators, including receptor-like kinases, transcription factors, and phytohormones, function in an integrated manner to ensure proper tissue differentiation and reproductive success. Advances in molecular genetics and genomics continue to deepen our understanding of these processes, offering potential applications in crop improvement, hybrid seed production, and fertility regulation.

Future research integrating multi-omics approaches, including transcriptomics, proteomics, metabolomics, and single-cell sequencing, together with CRISPR/Cas-mediated genome editing, is expected to further elucidate the molecular mechanisms underlying stamen development. These emerging technologies will facilitate the identification of novel regulatory genes and signaling networks, enabling precision breeding strategies for enhanced pollen fertility, hybrid seed production, and climate-resilient crop development. Continued integration of molecular

genetics, functional genomics, and comparative evolutionary studies will strengthen our understanding of male reproductive development and support sustainable agricultural production under changing environmental conditions.

5 Materials and Methods

5.1 Literature survey and data sources

The present study is based on a comprehensive review of published literature related to stamen and anther development in angiosperms. Peer-reviewed research articles, review papers, and experimental studies were collected from standard scientific databases, including Google Scholar, PubMed, and Web of Science. Emphasis was placed on studies involving *Arabidopsis thaliana* as a model system, along with comparative data from other plant species such as *Salvia* and *Gerbera*.

5.2 Selection criteria

Relevant studies were selected based on their focus on:

- Floral organ identity and the ABC/ABCDE model
- Genetic regulation of stamen development
- Anther ontogeny and cellular differentiation
- Role of receptor-like kinases and transcription factors
- Hormonal regulation of reproductive development

Only studies providing clear experimental evidence on gene function, signaling pathways, and developmental processes were included.

5.3 Data extraction and organization

Information from selected studies was systematically extracted and categorized into key thematic areas, including:

- Floral organ identity genes (A, B, C, D, E classes)
- Stages of anther development
- Molecular regulators (e.g., SPL/NZZ, EMS1, BAM1/2, RPK2, CIKs)
- Signaling pathways (MAP kinase pathways, receptor kinase signaling)
- Hormonal regulation (jasmonic acid, gibberellins, auxins)

The extracted data were organized to establish a logical sequence from early stamen specification to late-stage pollen development.

5.4 Comparative analysis

Comparative evaluation was performed across different plant species to identify conserved and divergent mechanisms of stamen development. Gene expression patterns and functional studies in *Arabidopsis*, *Salvia*, and *Gerbera* were analyzed to highlight evolutionary conservation and species-specific variations.

5.5 Synthesis of information

The collected data were critically analyzed and integrated to construct a unified framework describing the molecular and genetic regulation of stamen development. Special attention was given to linking classical genetic models (ABC model) with recent findings in signaling pathways and genomics.

5.6 Limitations

As this study is based on previously published data, no new experimental work was conducted. The conclusions are therefore dependent on the accuracy and scope of the cited literature.

Author's Contributions

RC conceived the review topic, designed the structure of the manuscript, conducted the literature review, performed literature collection and critical analysis, synthesized the published findings, prepared the figures and tables, and wrote, revised, and approved the final version of the manuscript.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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